Notes on Bolivian Mammals. 7. A New Species of *Abrocoma* (Rodentia) and Relationships of the Abrocomidae

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ABSTRACT

A new species of *Abrocoma* (Rodentia, Hystricognathi) from central Bolivia is described and compared with the three other species currently recognized. The relationships of *Abrocoma* to other hystricognath rodents are uncertain. A set of derived characters support recognition of the family Abrocomidae. Although usually placed within the Octodontoidea, the Abrocomidae may belong with the Chinchilloidea. A proposed phylogeny illustrates possible relationships within and between these two superfamilies.

RESUMEN

Una nueva especie de *Abrocoma* (Rodentia, Hystricognathi) de Bolivia central es descrita y comparada con otras tres especies actualmente reconocidas. La relación de *Abrocoma* con los otros roedores hystricognath es incierta. Una serie de carácteres derivados apoyan el reconocimiento de la familia Abrocomidae. Aunque usualmente se incluyen dentro de los Octodontoidea, los Abrocomidae pueden pertenecer a los Chinchilloidea. Una proposición filogénetica ilustra la relación posible dentro y entre estas dos superfamilias.

INTRODUCTION

The rodents of the genus *Abrocoma* have been placed in the subfamily Abrocominae of the Echimyidae (Ellerman, 1940) or of the Octodontidae (Landry, 1957), or as the family Abrocomidae (Cabrera, 1961; Patterson and Wood, 1982). This family has been allied

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TABLE 1
External Measurements (in millimeters) of *Abrocoma*
(Mean and standard deviation are given for each dimension with the minimum and maximum measurements in parentheses)

Variable	*A. bennetti bennetti*	*A. bennetti murrayi*	*Abrocoma cinerea*	*Abrocoma boliviensis*
N	13	12	9	2
	48.4 ± 34.9	367.8 ± 28.2	281.1 ± 28.9	315.0
	(278–393)	(328–405)	(228–321)	(310–320)
			n = 8	
Head and body length	205.9 ± 20.4	211.8 ± 16.3	197.3 ± 10.5	174.0
	(170–232)	(177–233)	(173–211)	(170–178)
Caudal length	142.5 ± 15.7	155.9 ± 16.3	83.3 ± 20.3	141.0
	(108–166)	(130–178)	(55–120)	(132–150)
			n = 8	
Hind foot length	35.6 ± 2.5	34.6 ± 1.8	27.8 ± 2.0	30
	(32–40)	(31–38)	(23–30)	(30)
Ear length	32.7 ± 2.7	no data	27.6 ± 1.7	22.5
	(28–35)		(25–30)	(20–25)
	n = 4			

with the Chinchillidae (Miller and Gidley, 1918) or placed in the Octodontoidea (Carleton, 1984; Reig, 1986). This history suggests both the distinctness of *Abrocoma* and the uncertainty of relationships of caviomorph rodents at the level of the family.

At least 10 names for living species of *Abrocoma* have been proposed, beginning in 1837 when Waterhouse named the genus, but recently these have been considered to be subspecies or synonyms of only two species, *A. bennetti* and *A. cinerea* (Ellerman, 1940: 154; Cabrera, 1961: 557; Honacki et al., 1982: 585; and Woods, 1984: 430). A third species, *Abrocoma oblativa* (Eaton, 1916), is known from an Inca burial site at Machu Picchu in Peru, but has not been found alive.

Two specimens of *Abrocoma* from the vicinity of Comarapa in central Bolivia have been in collections since 1926 and 1955, unstudied and unidentified to species. These specimens are conspecific and are here described and named as a new species of *Abrocoma*.

METHODS

Our methods are simple and traditional. There are only two specimens of the new species of *Abrocoma* and they are clearly different from other known species. We describe and illustrate these differences. Attempts (in 1984 and 1987) to obtain additional specimens in order to learn more about the habitat

of this new species and to get material in addition to skins and skulls for study were unsuccessful. Neither chromosomal nor genetic data have been published for any *Abrocoma,* however initial data on *A. bennetti* will soon be available (Contreras et al., in press).

Dimensions measured for tables 1 and 2 are:

1. Total length. Length from tip of nose to end of last caudal vertebra as measured by the collector in the field.
2. Head and body length (HB). Obtained by subtracting the collector's field measurement of caudal length from the total length.
3. Caudal length (TAIL). Collector's field measurement of length of tail from end of last caudal vertebra to point where tail joins the body as measured from the basal flexure of the spinal column.
4. Length of hind foot (HF). Measured from end of heel to end of most distal claw by collector in the field.
5. Ear length (EAR). Measured by collector in the field from the basal notch to distalmost edge of ear.
6. Condylobasal length (CBL). Measured from anterior edge of premaxillaries to posterior edges of condyles.
7. Modified basal length (BSL). Length of skull from anterior edge of incisor at the alveolus to anteriormost edge of foramen magnum.
8. Palatilar length (PLR). Standard measurement from posterior incisive alveolar margin to anterior margin of mesopterygoid fossa.
9. Bullar length (BUL). Length of line, parallel to long axis of the skull, from anteriormost exposed edge of bulla to posterior edge of bulla.
10. Bullar width (BUW). Greatest width of exposed bulla perpendicular to bullar length.
11. Bullar bulb width (BBW). Width of bulla perpendicular to axis of skull and excluding exposed auditory tube.
12. Alveolar length of upper molariform tooth row (ALV). From most anterior alveolar margin to most posterior alveolar margin.
13. Occlusal length (OCL). Greatest length of planar or grinding surface of the upper molariform tooth row.
14. Dental span (DS). Greatest width between external edges of molar tooth rows.
15. Zygomatic breadth (ZYG). Greatest width of skull across zygomatic arches.
16. Interorbital breadth (IOB). Smallest distance between internal edges of orbits across top of skull.
17. Nasal length (NAL). Greatest length of exposed nasal bones on top of rostrum.
18. Width of rostrum (ROW). Measured just anterior to base of zygomatic arch.
19. Braincase depth (BCD). Height of skull when resting on a flat surface, measured from that surface to the parieto-frontal suture on the top of the braincase.
20. Length of palate (PAL). From posterior margin of incisive foramina to anterior margin of mesopterygoid fossa.

TAXONOMY

As *Abrocoma* has been studied little, it is desirable to summarize the taxonomic context of this genus and to point out some postulated relationships and unresolved problems. The taxonomic arrangement below largely follows that of Carleton, 1984.

ORDER RODENTIA BOWDITCH, 1821

There is general agreement that the rodents are a distinct monophyletic group. Rodent synapomorphies relate mainly to specializations for gnawing and include the separation and distinction of incisors and cheekteeth, a longitudinal and open glenoid fossa so these sets of teeth can operate separately, and other characters. A comprehensive review and summary of the current state of knowledge of rodent evolution was published recently (Luckett and Hartenberger, eds., 1984; for a detailed diagnosis of the order and references to earlier works see also Carleton, 1984).

SUBORDER HYSTRICOGNATHI TULLBERG, 1899

A bipartite division of rodents proposed by Tullberg was used in the monumental review of rodents by Ellerman (1940). The monophyly of one of these branches, the Hystricognathi, is supported by considerable data (see discussions by Wood, 1984: 478; by Woods and Hermanson, 1984: 515; and references in Carleton, 1984: 263), although the relationships of some additional groups to the Hystricognathi are controversial (Lavocat and Parent, 1984).

The most commonly cited synapomorphies of Hystricognathi relate to the lower jaw. The base of the angular process is laterally placed, resulting in a distinct hystricognath groove on the ventral surface be-

tween the angular process and the capsule of the base of the lower incisor. Certain features of fetal membrane morphology support the monophyly of this suborder (Luckett, 1984). Additional characters of myology (Woods and Hermanson, 1984), cephalic arteries (Bugge, 1984), tooth structure (Hartenberger, 1984), and perhaps the intromittent sac of the glans penis (Spotorno, 1979) largely support this grouping.

The International Code of Zoological Nomenclature does not now deal with names of taxa above the family-group level. It may be noted, however, that the name Hystricina of Waterhouse (1839: 92) would apply if priority were a determining factor, and Lee A. Spencer (1987) chose to use this name.

INFRAORDER CAVIOMORPHA
KRAGLIEVICH, 1930

These are the New World families. Whether they comprise a monophyletic group is unclear. Woods (1982: 377) suggested that the use of Caviomorpha as a taxonomic designation be discouraged. Earlier hypotheses relating African Petromuridae with South American Octodontidae were reviewed and rejected by Landry (1957) but considered more favorably by Woods and Hermanson (1984). The other Old World hystricognaths (Hystricidae, Bathyergidae, and Thryonomyidae) are relatively distinct from each other and from the American families. These are negative reasons, in that they fail to associate Old World families with specific New World families. Positive reasons (other than continental sympatry) are needed to associate New World families with each other, namely sets of synapomorphies that unite all or some of the diverse American families. The Erethizontoidea were treated as a sister group of the other caviomorph superfamilies by Hartenberger (1984: 29) and the African Thryonomyidae and Petromuridae were included in the same clade with five of the South American families of hystricognaths by Woods and Hermanson (1984: 540). The albumin-based phylogeny depicted by Sarich and Cronin (1980) also suggested a relationship between the Petromuridae and Bathyergidae of Africa and the South American Echimyidae, Myocastoridae, and Octodontidae, but Sarich (1984: 430) later expressed less confidence in

these relationships, based on statistical grounds. The lack of a clear consensus indicates that more work is needed at this level.

SUPERFAMILY OCTODONTOIDEA
WATERHOUSE, 1839

Although Waterhouse used the family name Octodontidae, Simpson (1945: 97, 212) first used the superfamily name. He included the families Capromyidae, Octodontidae, Ctenomyidae, Abrocomidae, Echimyidae, Thryonomyidae, and Petromyidae in the superfamily Octodontoidea, but did not provide diagnostic characters for it. Landry (1957) characterized the superfamily as having: "Cheek teeth hypsodont . . . with wear assume pattern of folds or lakes. Skulls usually heavy. Incisors usually broad and deep. Masseteric ridge on mandible usually wide and shelflike. Paroccipital processes often long. Lateral process of supraoccipital and paroccipital process usually closely appressed with little of mastoid showing between them." He included the families Cuniculidae (= Agoutidae), Heptaxodontidae, and Dinomyidae, as well as the Octodontidae (with Abrocominae as a subfamily).

Hypsodont (= hypselodont in this case) cheek teeth occur also in Chinchilloidea and Cavioidea and "folds or lakes" seems to apply equally well to these two superfamilies also. Skulls of *Abrocoma* are relatively lightly built, certainly not "heavy," nor are skulls especially heavy in the Octodontidae (except for *Ctenomys*). Incisors of *Abrocoma* are noticeably slender and those of Octodontidae (again excluding *Ctenomys*) are only moderately broad and deep. Even the burrowing octodontid genus *Spalacopus* has incisors that are relatively thin compared to those of *Ctenomys*. The masseteric ridge referred to is along the lower edge of the angular process (the lateral masseter inserts here). This masseteric ridge is present in a number of families of Hystricognathi. The ridge is present only near the base of the angular process in *Abrocoma*, however, in association with the elongate and slender form of the process. A different enlarged ridge is present ventrolateral to the insertion of the medial masseter below the toothrow in the Caviidae and Hydrochaeridae. The paroccipital processes of Octodontidae are not especially long, nor are those of

Abrocoma. They are "long" in *Myocastor* (extremely so) and in *Dinomys* (moderately so). The statement about lateral processes of supraoccipital does not apply to Octodontidae or to Abrocomidae, all of which have relatively enlarged bullae (to different degrees) that are widely exposed posterolaterally between the lateral supraoccipital and paroccipital processes.

Turning to Landry's characterization of the Chinchilloidea we find: "Cheek teeth hypsodont . . . Cement in folds at least in some forms. Later forms with cheek teeth composed of tightly appressed cross laminae; no cement." The nonuniqueness of hypsodonty has been commented on above. Cement occurs also to some degree in the folds of those Octodontidae that retain reentrant angles as well as in Abrocomidae (fig. 1). The words "no cement" in reference to "later forms" (i.e., Chinchillidae) are not correct (fig. 1B), as described below.

Landry (p. 58) emphasized the questionable status of Abrocominae by commenting "This subfamily quite possibly does not belong in the family [Octodontidae]." Earlier (pp. 50–51) he had outlined characters shared with octodontids, primarily "the zygomatic masseteric fossa and the slim, angular process of the mandible," and others shared with *Chinchilla*, including "an exaggerated expansion of the bullae, a narrow palate with the internal nares extending forward between the tooth rows, and . . . a rabbitlike rostrum with a long diastema and narrow, sharply recurved incisors." He retained *Abrocoma* in a subfamily of Octodontidae, but noted "it is still possible that *Abrocoma* is the modified descendant of [an] ancient chinchilloid stock."

Reig (1986: 419) stated that "Abrocomids are . . . closely related to octodontids . . . [and] are a distinct offshoot of the octodontoids . . . [that evolved] in Upper Miocene or Early Pliocene times" but he did not note characters that support this taxonomic hypothesis.

Lee A. Spencer (1987) provided a review of fossil Abrocomidae and Octodontidae and postulated a phylogeny. Some questions arise in regard to this phylogeny. Beginning with the Octodontidae (and working backward in the phylogeny), the Abrocomidae were postulated to be a sister group of the Octodontidae (including the Ctenomyinae). [This clade corresponds to clade 1 in our figure 4 except for the exclusion of the Chinchillidae]. The Capromyidae are a sister group of the preceding and the complete clade at this level is considered to be the Octodontoidea. The occurrence of hypselodonty is the only character given in the diagnosis of the Octodontoidea.

Hypselodonty has developed many times independently in different orders of mammals and in different families of rodents, so the possibility that the present assemblage, based on this character alone, is polyphyletic rather than monophyletic should not be dismissed entirely. Additional synapomorphies are needed to support the monophyly of the Octodontoidea as postulated by Spencer. Hypselodonty occurs also in Caviidae, Chinchillidae, and Capromyidae. All of these groups need to be fitted into a total phylogeny of caviomorph rodents.

In Spencer's phylogeny, the Echimyidae and perhaps the Myocastoridae are the next sister group(s) and the synapomorphy uniting the clade at this level is the retention of the first developed fourth premolar (rather than its shedding and replacement by another tooth). The Erethizontidae are the next sister group. (The loss of a mental foramen and the presence of lateral processes on the supraoccipital are said to be uniting synapomorphies at this level.)

Presumably the presence of a mental foramen in the Chinchillidae is grounds for excluding them from the phylogeny as described above. However, one of the three living genera of chinchillids, *Lagostomus*, seems to lack the mental foramen. A mental foramen is well developed in *Lagidium* (fig. 2B) and the foramen is only slightly smaller in *Chinchilla* (fig. 2A). As a plausible alternative to Spencer's interpretation, we postulate a secondary development of the foramen (in clade 7 of our fig. 4), rather than the exclusion on the basis of this one character of chinchillids from consideration as relatives of octodontids at the family group level.

In *Lagostomus* many foramina perforate the dentary (fig. 2G shows the lingual surface, and another cluster of foramina extends along the ventral surface of the dentary). Similar clusters occur in the other two living chinchillid genera, *Chinchilla* and *Lagidium* (a
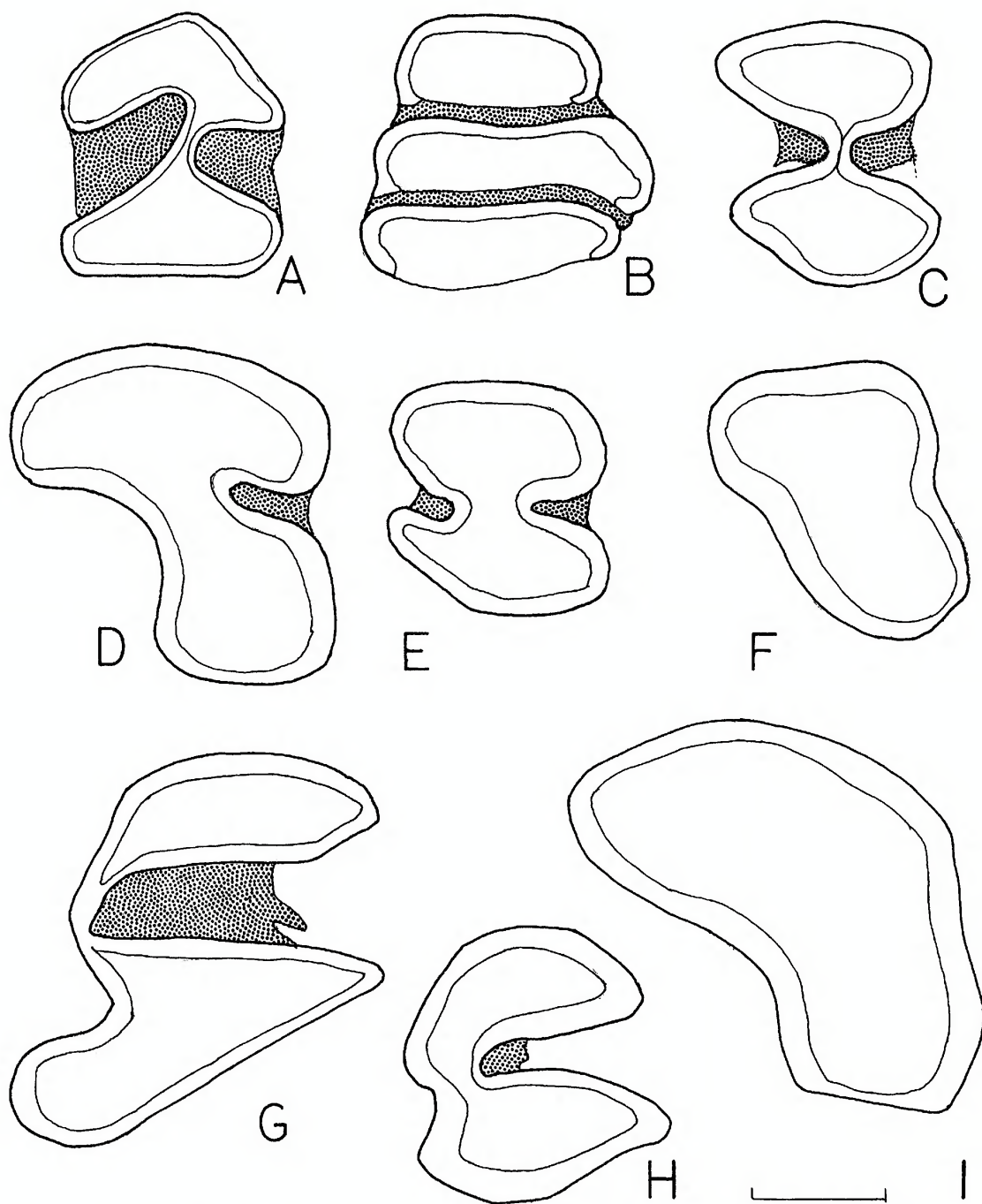
Fig. 1. Right P4 (labial side on the left) of various Octodontidae, Chinchillidae, Caviidae, and Abrocomidae, illustrating the presence of cement (stippled) in reentrant enamel folds of each of these families. All of the molariform teeth in a tooth row tend to have the same pattern. **A.** *Abrocoma* n. sp. (BM 34.9.2.171), **B.** *Chinchilla lanigera* (AMNH 148465, young), **C.** *Aconaemys fuscus* (AMNH 91655), **D.** *Octodon degus* (MVZ 150072), **E.** *Spalacopus cyanus* (AMNH 33277), **F.** *Octodontomys gliroides* (AMNH 249052), **G.** *Cavia aperea* (AMNH 260799), **H.** *Microcavia niata* (AMNH 263000), and **I.** *Ctenomys frater* (AMNH 263011). Scale at lower right represents 1 mm.
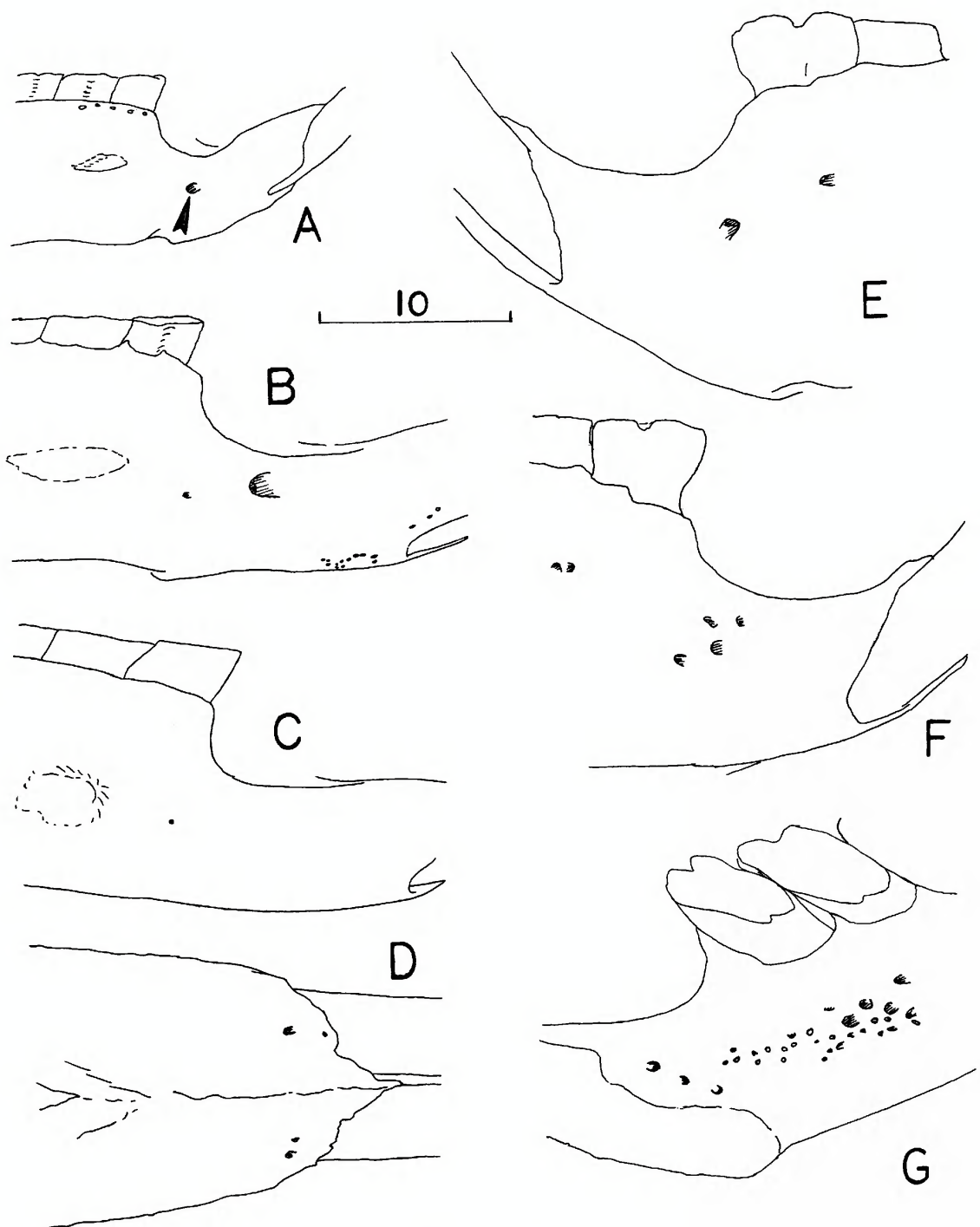
Fig. 2. Foramina in dentaries. **A.** *Chinchilla* (AMNH 148463, labial side of right dentary). **B.** *Lagidium* (AMNH 260946, labial side of right dentary). **C.** *Lagostomus* (AMNH 262286, labial side of right dentary). **D.** *Lagostomus* (AMNH 262285, dorsal surface at incisive alveoli). **E.** *Coendou* (AMNH 130368, labial surface of left dentary). **F.** *Coendou* (AMNH 130368, labial surface of right dentary). **G.** *Lagostomus* (AMNH 246958, lingual side of right dentary). Scale represents 10 mm; all to same scale.
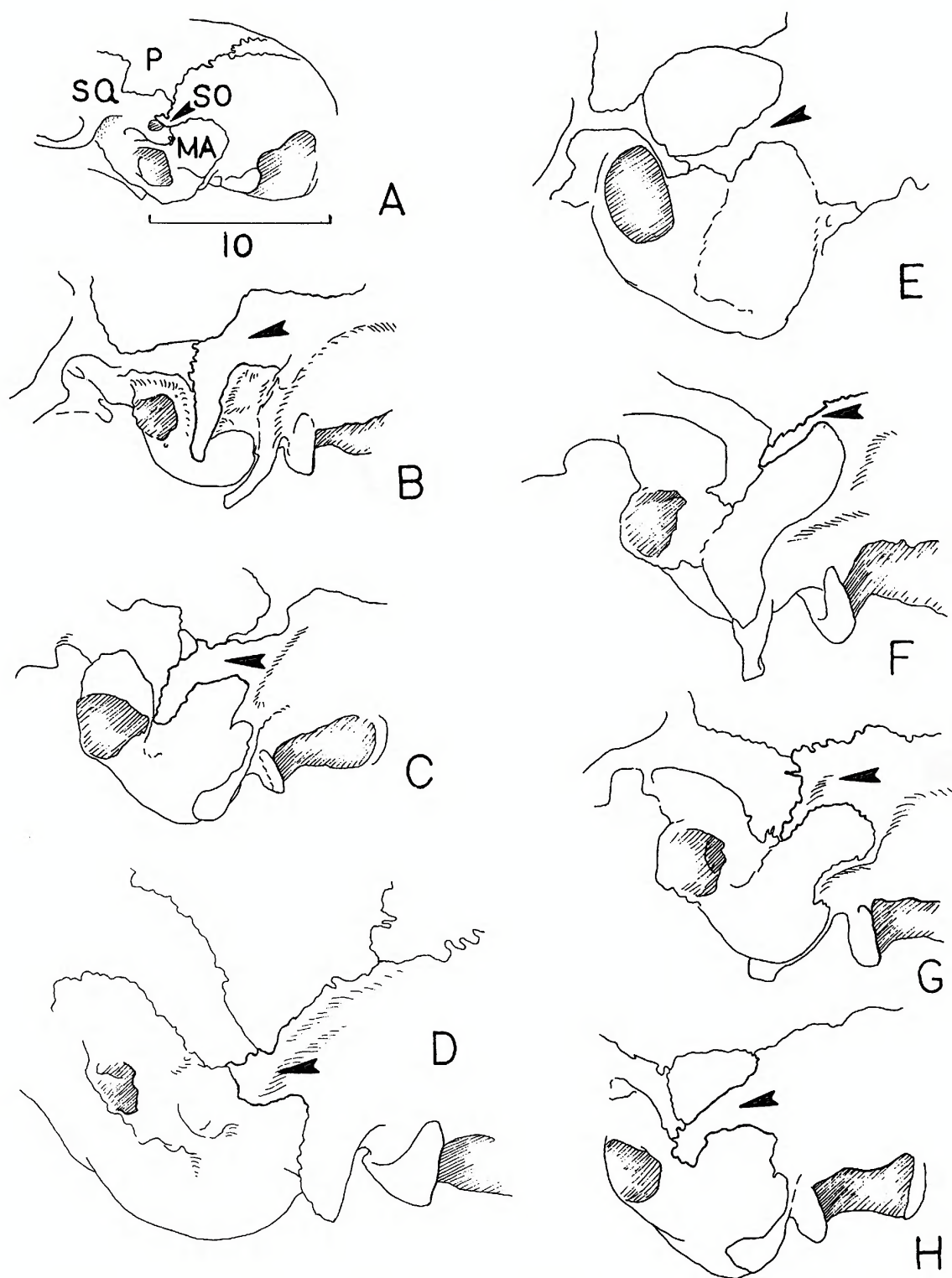
Fig. 3.   Degrees of development of lateral supraoccipital processes in skulls of various rodents. **A.** *Oxymycterus paramensis* (MVZ 119947, a myomorph, family Muridae; labeled elements are **SO** supraoccipital, **MA** mastoid, **P** parietal, and **SQ** squamosal). **B.** *Proechimys* (AMNH 137221, family

few of the ventral foramina are visible in fig. 2B). In *Lagostomus* (and in contrast to *Chinchilla* and *Lagidium*), no medium-to-large foramen that transmits nerve fibers is regularly present on the labial side of the bone in the area below the anterior end of the molariform tooth row (the usual definition of a mental foramen being something like this in regard to size, function, and position). To our knowledge no specimen of *Lagostomus* has been dissected to establish whether nerves pass through any of these foramina or not. (Of course this is also true of the vast majority of species in which unquestioned mental foramina occur.) The occurrence of such a foramen is general in most groups of mammals, including rodents other than those being discussed here, and its loss is probably a derived or synapomorphic character for some groups. Possibly it has been lost more than once in different phyletic lineages. Some, but not all, specimens of *Lagostomus* have a small foramen on the labial side of the dentary (about 0.03 mm in the right jaw of AMNH 262286, for example; fig. 2C). Sometimes this is present in both left and right dentaries and sometimes in only one dentary. In comparison, figure 2B shows a specimen of *Lagidium* with both a typical mental foramen and a small foramen in about the same position as the small one in figure 2C. In a few specimens of *Lagostomus* (fig. 2D) a pair of small foramina occur on the dorsal surface just behind the incisive alveoli. Which, if any, foramina transmit nerves is unknown.

The Erethizontidae were said to lack the mental foramen. Foramina present in the diastemal area of the dentary bone were interpreted as "always small and often numerous, quite unlike the true mental foramen." Examination of a number of skulls of *Erethizon* (10), *Coendou* (10), and *Echinoprocta* (5) in the American Museum of Natural History shows that at least one foramen is present, generally in the same part of the diastemal area. The size is somewhat variable.

Smallness is a concept that needs quantification for comparison to be useful. The mental foramen in the left dentary of one *Erethizon dorsatum* (AMNH 120848) is 0.5 mm in its smaller dorsoventral dimension. In some other specimens the foramen is smaller than 0.5 mm and sometimes additional foramina are present. Small foramina of variable position were considered by Spencer generally to be "nutritive" foramina that transmit blood vessels. Variation in one individual of *Coendou* is illustrated (fig. 2E left side, F right side). One specimen of *Coendou bicolor simonsi* (AMNH 262273, head preserved in alcohol) was dissected (by Anderson) to see if nerves passed through the mental foramina. Clearly they do. In conclusion, although there is some variability in size and position, Erethizontidae do have mental foramina.

The only other synapomorphy noted for the clade uniting Erethizontidae and the other families noted above was the presence of a lateral process on the supraoccipital. Although this character was not defined, illustrated, described, or otherwise discussed in Spencer's presentation, it had been used as early as 1887 by Winge and was discussed and illustrated by Landry (1957: 41) in comparisons of *Myocastor* and *Capromys*. The condition of the lateral process was also mentioned in most of the family accounts of Woods (*in* Anderson and Jones, 1984), but some of these brief statements need qualification or amplification.

Examination of selected specimens (from one to six specimens of each genus mentioned, depending on availability, in the American Museum of Natural History) provides the basis for the following comments. The degree of development of a lateral process of the supraoccipital varies (fig. 3), and there is no clear dichotomy between its presence and its absence. A small lateral process is present in many rodents other than caviomorphs (for example, fig. 3A shows *Oxy-*

←
Echimyidae). **C.** *Octodontomys gliroides* (AMNH 249052, Octodontidae). **D.** *Coendou mexicanus* (AMNH 28334). **E.** *Chinchilla lanigera* (AMNH 148465, Chinchillidae). **F.** *Cavia aperea* (AMNH 149996, Caviidae). **G.** *Microcavia niata* (AMNH 263000, Caviidae). **H.** *Abrocoma cinerea* (MVZ 150117, Abrocomidae). Arrows are at the base of the lateral supraoccipital process in each drawing. The scale below A represents 10 mm. All are to the same scale.

mycterus, a myomorph of the family Muridae).

The greatest development is seen in Echimyidae (fig. 3B shows *Proechimys*) and Octodontidae (including Ctenomyidae; fig. 3C shows *Octodontomys*) in which the process extends to the squamosal process, as is generally true, and then turns conspicuously downward. Woods (1984: 424, 428) referred to a "slight lateral supraoccipital process" in both Ctenomyidae and Octodontidae. This seems slightly misleading to us.

Long and downturned processes also occur in *Myocastor.* They occur in Echimyidae (*Haplomys, Proechimys, Trichomys, Dactylomys, Isothrix,* and *Echimys* were examined). This condition occurs in Octodontidae (*Octodon, Octodontomys, Aconeamys,* and *Spalacopus* were examined). It occurs in Capromyidae (*Capromys, Geocapromys,* and *Plagiodontia*) in which the lateral process of the supraoccipital is relatively long, distally downturned, and terminally rounded. The paroccipital process of the exoccipital is generally large and elongate and is separated from the lateral process of the supraoccipital by a characteristic narrow slot. These two elements are so fused that their common boundary is not distinguishable as is generally the condition in caviomorphs. The supraoccipital extends onto the dorsal surface of the skull anterior to the lambdoidal crest and the suture is obliterated by fusion with the parietals. Whether there is a separate interparietal ossification that is also fused with the preceding is not clear in the specimens examined.

We have not reviewed the condition in specimens of the Heptaxodontidae (extinct) but skulls of *Elasmodontomys* (Anthony, 1918: 382) seem consistent with the previous description for Capromyidae, so far as the features are visible in the figures.

A relatively long and downturned lateral process occurs in *Acanthion* among the Hystricidae (for which family Woods, 1984: 402, had noted a "distinct" lateral process).

In Caviidae, a process of moderate length lies above a dorsoventrally elongate exposure of the mastoid. (Figure 3F shows *Cavia* and 3G shows *Microcavia* with its more enlarged auditory bullae.) Woods (1984: 412) noted "lateral process of supraoccipital lacking." Whether this was simply a mistake or wheth-

er he was restricting the concept to exceptionally long processes like those in figures 3B and C is not certain.

In the Erethizontidae (fig. 3D shows *Coendou*), Woods (1984: 402) regarded the lateral process as "distinct." We might say "of moderate length."

In Dinomyidae (only the living *Dinomys* was examined), the interparietal and supraoccipital tend to fuse even in young animals although the supra- and exoccipitals seem not to fuse as early as those of most other caviomorphs. The posterior squamosal process is noticeably shorter than in other related families but the supraoccipital contacts the process laterally and the exposed surface of the supraoccipital thus appears as a sort of lateral process. Woods (1984: 412) reported it as "lacking."

In Dasyproctidae, the squamosal process is enlarged and the supraoccipital process correspondingly reduced. The supraoccipital is unusual in extending on the top of the skull anterior to the lambdoidal crest. This relatively broad flange joins the squamosal and mastoid laterally and its most lateral projection might or might not be recognized as a process. Woods (1984: 410) reported the process as "lacking."

In Agoutidae, the squamosal process is also enlarged and the supraoccipital correspondingly reduced. Woods (1984: 420) reported it as "lacking."

In Abrocomidae (fig. 3H shows *Abrocoma cinerea*), the process is relatively longer than in 3D but not so long as in 3B or 3C. *Abrocoma cinerea* has larger bullae than other species of the genus and may be compared with *Chinchilla* (fig. 3E), the chinchillid genus with most enlarged bullae. The lateral process in Abrocomidae seems more like that of Chinchillidae than like the process in Octodontidae or Echimyidae.

In spite of the diligent efforts of Landry and other workers since 1957 (e.g., Wood and Patterson, 1959; Woods, 1984; various contributors to Luckett and Hartenberger, 1984; and Spencer, 1987), no clear diagnosis (including a set of synapomorphies) exists to support the hypothesis of monophyly for the Octodontoidea. Nor is it certain that the Abrocomidae belong in this superfamily rather than the Chinchilloidea, as suggested (but dismissed) by Landry above. The first
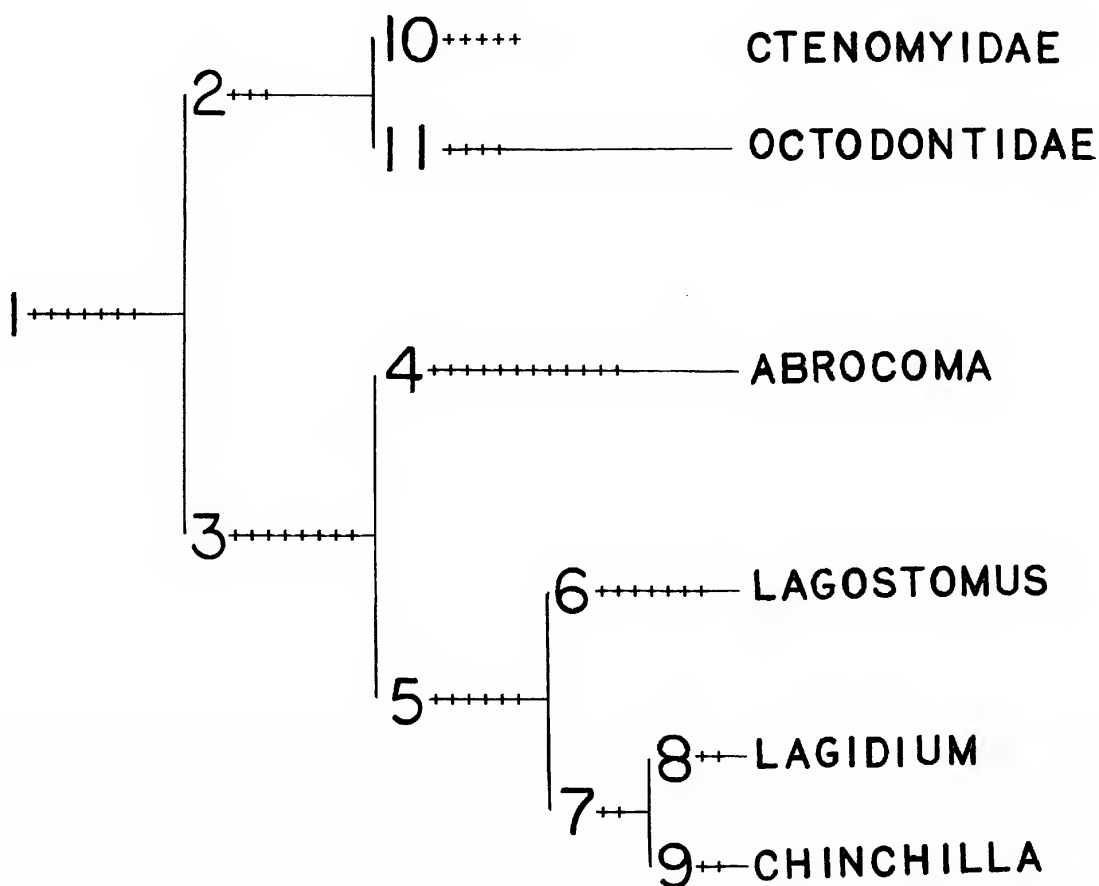
Fig. 4. Postulated phylogeny discussed in text. Characters are given in text for each of the numbered clades. The numbers of postulated synapomorphies for each clade are shown by small cross bars.

relevant family-group name was Chinchillidae Bennett, 1833; the first use as a superfamily was by Kraglievich, 1927. To ask whether Abrocomidae are Octodontoidea or Chinchilloidea reflects the common assumption that these superfamilies are real in some sense. However, since the characters, the content, and the monophyly of the Octodontoidea and Chinchilloidea are all unclear, a more basic and useful question is "what are the relationships among the various groups of caviomorphs?" This question in its entirety is too large to answer here. Additional studies are needed to establish more satisfactory hypotheses of relationships.

Nevertheless, we feel that it will be helpful to illustrate the nature of this problem by outlining a preliminary hypothesis of relationships of Abrocomidae. The phylogeny shown in figure 4 is postulated on the basis of synapomorphies (under 1 below) that distinguish this clade from more primitive, brachydont "octodontoids." Reig (1986) offered the Echimyidae as ancestral prototypes for many South American hystricognath groups. Assuming such an outgroup, consider the following synapomorphies (each number refers to the clade beginning with that number in figure 4 and the characters listed under each number are postulated to be synapomorphies of the clade at that level):

1. (a) Teeth persistent in growth (= hypselodont, Woods, 1982: 377)
   (b) Occlusal surface of cheekteeth wears flat
   (c) Bullae large
   (d) Foramen or depression present ventrally where auditory tube joins rounded bulla
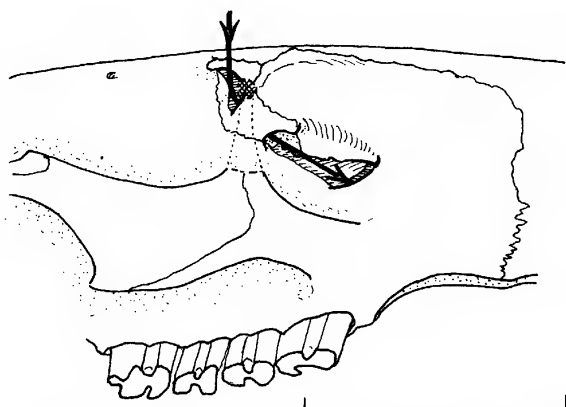
Fig. 5. Lacrimal canal opening onto side of rostrum (in *Abrocoma bennetti,* MVZ 118669). Scale represents 10 mm.
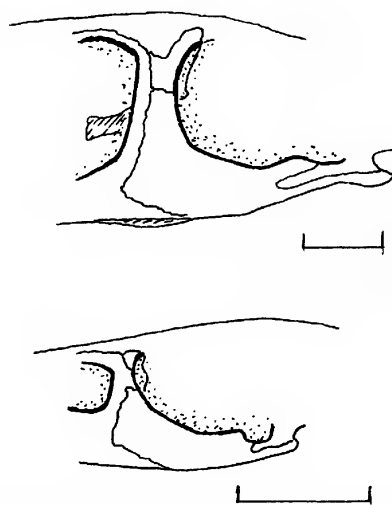

Fig. 6. Anterior zygomatic region of chinchillids for comparison with octodontids (in fig. 7) and abrocomids (in fig. 8). *Lagostomus maximus* (above) and *Chinchilla lanigera* (below). Note the dorsal extension of jugal, which is in actual contact with the lacrimal in *Lagostomus* and *Lagidium.* Scale represents 10 mm.

    (e) Paroccipital process moderate in size and length and adhering to or close to the bulla

    (f) Pterygoid delicate, adjacent foraminae enlarged, especially those near basisphenoid

    (g) Pes ctenodactyloid, specialized distal long thickened hairs on digits, especially D2 to D4, tending to form linear hair-comb above claw on at least D2

2. (a) Mesopterygoid fossa anteriorly attenuate and reaching level of anterior margin of M2 (or posterior half of M2 in *Spalacopus*)

    (b) Incisive foramen widened anteriorly and relatively short

    (c) Cheek teeth simplified to figure 8 or kidney shaped above and below

3. (a) Rostrum narrowed

    (b) Lophs of cheek teeth transverse in orientation

    (c) Two lophs per upper tooth

    (d) Well-developed inflected angles of mandible

    (e) Coronoid process of mandible low

    (f) Angular process elongate and slender

    (g) Angular process tending to be subhystricognath, i.e., nearly parallel, less divergent posteriorly and laterally

    (h) Incisors shortened

    (i) All or part of the lacrimal and maxillary bones lateral to the posterodorsal part of the lacrimal canal lost, thus canal open laterally on maxillary, anterior to the zygomatic arch (fig. 5)

4. Characters summarized below (as 1 to 12) under the genus *Abrocoma*

5. (Chinchillidae)

    (a) D1 of pes reduced

    (b) D5 of pes lost

    (c) Laminae of cheek teeth widened and fused

    (d) Enamel of anterior side of loph strengthened and posterior side weakened in uppers, and the reverse in lowers

    (e) Tail hair in two distinct tracts, long dorsal mane grading into shorter paler sides, and blackish tract of short hair on ventral surface

    (f) Jugal with a dorsal process contributing to bridge, in contact with lacrimal (fig. 6) in contrast to the plesiomorphic condition in Octodontoidea and Abrocomidae (figs. 7 and 8).

6. (*Lagostomus*)

    (a) D1 of pes lost

    (b) Toes and claws of pes enlarged and sturdy

    (c) Lophs reduced to two on most cheek teeth, the small posterior loph above and anterior loph below being lost
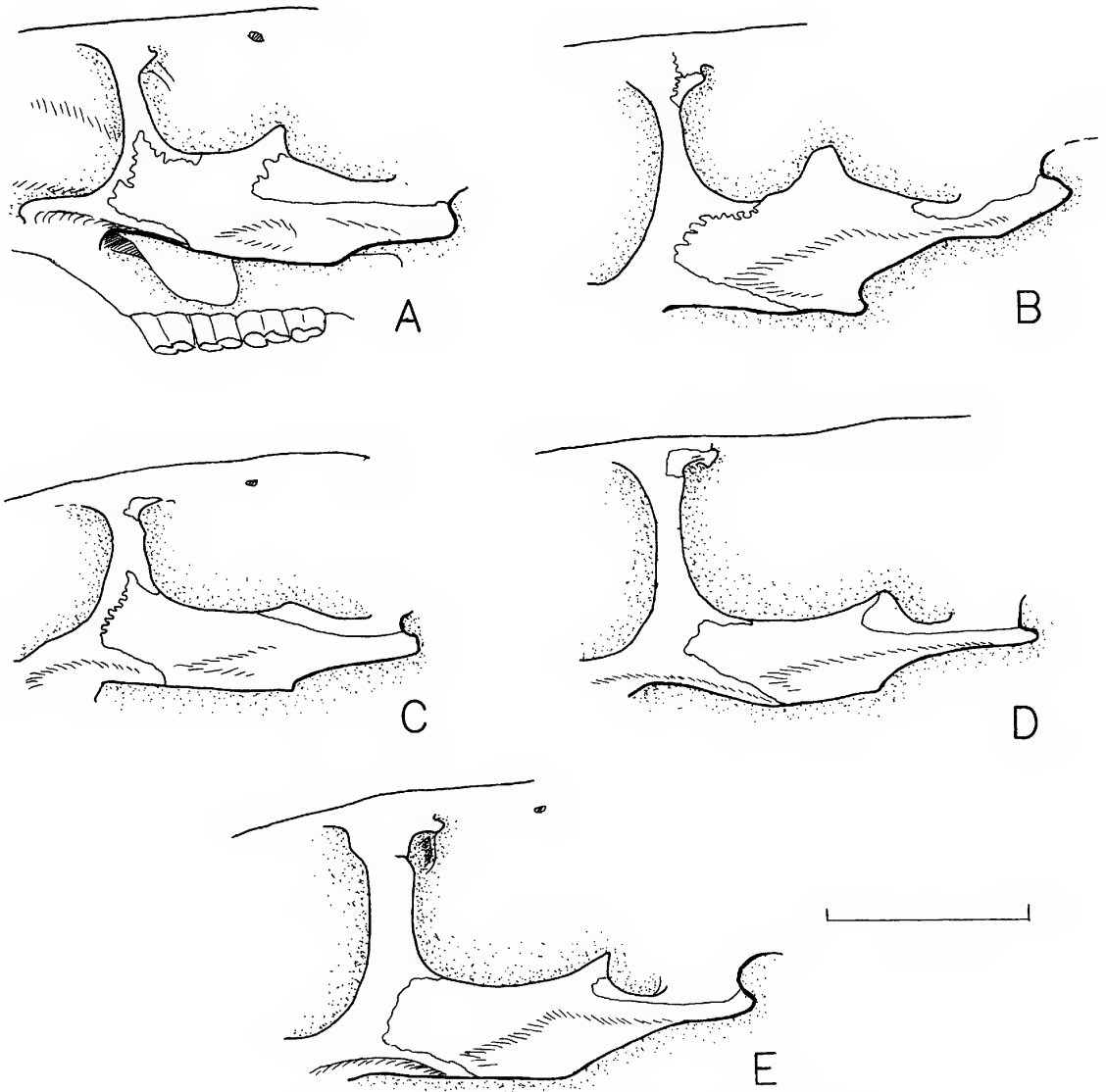
Fig. 7.   Anterior zygomatic area of octodontids. **A.** *Spalacopus cyanus* (AMNH 33277), **B.** *Ctenomys frater mordosus* (AMNH 263011), **C.** *Aconaemys fuscus* (AMNH 91655), **D.** *Octodontomys gliroides* (AMNH 249052), and **E.** *Octodon degus* (MVZ 150079). Scale represents 10 mm.

(d) Rostrum widened basally in association with larger chunkier skull generally

(e) Paroccipital process lengthened

(f) Mastoid excluded from dorsal exposure by enlarged posterior process of squamosal

(g) Pterygoid less delicate, foramina reduced, especially those near the basisphenoid bone

7. (a) Pelage especially fine and dense, suiting a cold climate

(b) Secondary redevelopment of mental foramina

8. (*Lagidium*)

(a) Lophs curved backward medially on uppers and forward laterally on lowers

(b) Pterygoid less delicate, foramina reduced, especially those near the basisphenoid bone

9. (*Chinchilla*)
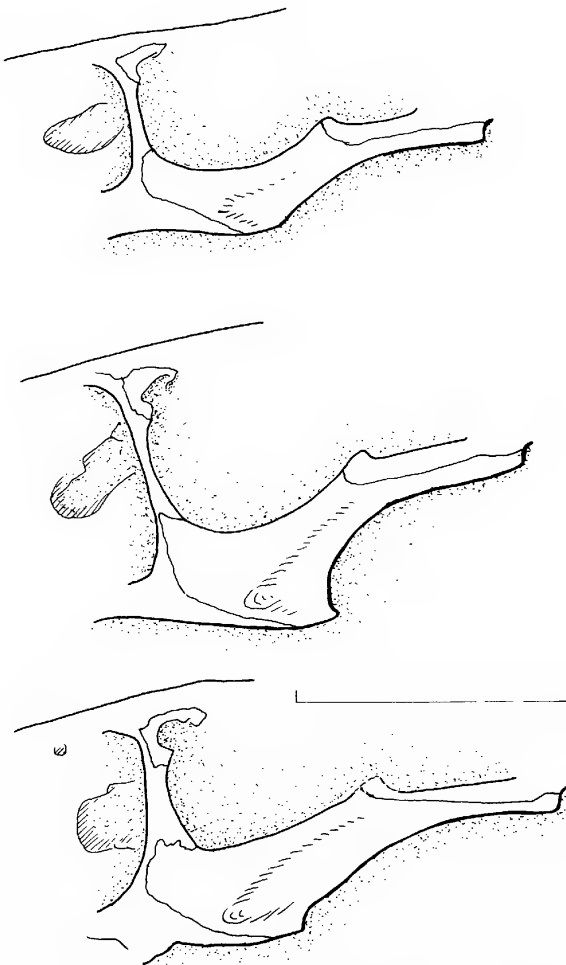
(a) Bulla further enlarged

Fig. 8. Drawings of anterior zygomatic area to show slender strutlike anterior zygomatic bridge, jugal confined to lower part of bridge, and relatively large lacrimal bone. From top to bottom, *Abrocoma* n. sp. (MVZ 120238), *A. bennetti* (MVZ 150117), and *A. cinerea* (MVZ 116801). Scale represents 10 mm.

(b) Jugal regressed, dorsal process not in contact with lacrimal
10. (Ctenomyidae)
   (a) Specializations for subterranean life similar to those of Geomyidae, including soft and short pelage, relatively broad rostrum, reduced eyes and ear pinnae, strong forefeet with long claws, tail of moderate length and moderately or poorly haired, usually well developed lambdoidal crest
   (b) Skull massive, with enlarged parie-

tal ridge, zygomatic arch enlarged and with pronounced upwardly projecting jugal process
   (c) Postorbital process on frontal
   (d) Bulla relatively large and pear shaped
   (e) Angular process of dentary widely spreading laterally
   (f) Cheekteeth simplified to kidney shape, M3 reduced in size
11. (Octodontidae; no striking synapomorphies; see Ellerman, 1940: 155 and 161; and Woods, 1984: 424 and 427)
   (a) Cheekteeth eight-shaped
   (b) Pollex and hallux somewhat reduced
   (c) Large penial spikes (Spotorno, 1979)

This will suffice to suggest the phylogeny represented by the cladogram shown in figure 4. Now, assuming this phylogeny for the moment, how should it be divided into superfamilies or should it be divided into superfamilies at all? A strictly cladistic approach might recognize the clade beginning with 3 as the superfamily Chinchilloidea and thus assign Abrocomidae to this superfamily. A more phenetic approach concerned with degrees of difference might single out the distinctive animals and features of the Chinchillidae (from 5 on up) and limit the superfamily to these, leaving the Abrocomidae in an uncertain state or in an admittedly paraphyletic superfamily Octodontoidea. Another alternative would be to use Chinchilloidea (an older name than Octodontoidea, based on Bennett's use of the family-group name Chinchillidae in 1833) for the entire clade (beginning at 1).

The phylogeny offered above assumes that certain characters of the Chinchillidae, assumed by previous workers to be plesiomorphic in that family, are derived from "octodontoid" patterns seen in *Abrocoma*. These include the narrow, ascending jugal lacking a zygomatic masseteric fossa. Both Landry (1957) and Patterson and Wood (1982) used these characters to separate chinchillids from *Abrocoma*, despite their other similarities. Both derive chinchillids from Oligocene or Miocene fossil groups that precede the appearance of abrocomids in the late Miocene. We encourage a reexamination of mid-Ter-

tiary fossil caviomorphs in the light of possible abrocomid-chinchillid relationships.

By making different assumptions about the sequences of changes and the relative importance of characters, a case could be made for switching the positions of the genera *Abrocoma* and *Lagostomus* in figure 4. This might be considered to place *Abrocoma* squarely in the middle of the family Chinchillidae. See notes relating to characters 4 to 8 under *Abrocoma* below.

In view of the different phylogeny postulated by Spencer (1987), the validity of the basal clade postulated here needs further testing by comparing its characters with those of other caviomorphs. Before changing the formal classification, an analysis of this sort needs to be extended to other characters and a greater variety of caviomorphs, especially other families previously included in the Octodontoidea. Ideally this analysis would include all living and fossil genera, although in practice this will not be possible because of missing data, for example from missing parts of most fossil specimens, and especially the absence of soft parts.

In addition to the different interpretations (e.g., of Wood, 1984, and Woods and Hermanson, 1984) regarding the possible monophyly of the Caviomorpha noted earlier, the diversity of unresolved possibilities is reflected in the placement of *Chinchilla* closer to *Erethizon, Agouti,* and *Dasyprocta* than to *Octodon* and the placement of the latter closer to three genera of Echimyidae and to *Myocastor* by Sarich (1984: 430) on the basis of albumin immunology. Sarich (p. 438) also noted that the chinchillid genus *Lagostomus* reacted no more strongly with *Chinchilla* than with other hystricognaths.

Sarich (1984: 430), however, discussed several statistical problems with his phylogeny, particularly the iterative procedure used. Of particular relevance here, we note that *Octodon* reacted almost as strongly with *Erethizon* antisera as with *Hoplomys* antisera, yet *Octodon* and *Hoplomys* are lumped together in one clade, and *Erethizon* is placed in a distant clade with *Chinchilla*. Other biochemical and morphological data suggest that chinchilloids and octodontoids may not be so distantly related as implied by the preceding. Beintema (1984), for example, found that

amino acid sequences of ribonuclease of *Chinchilla* are more similar to those of *Proechimys* than to those of *Cavia* and *Erethizon*. The hystricognath cladograms based on blood protein electrophoresis presented by Woods (1982) placed *Chinchilla* near or within the octodontoid assemblage. Bugge (1984) found the carotid arterial patterns of *Chinchilla* and *Octodon* to be very similar, differing in only one character, and to resemble each other more than those of other caviomorph superfamilies.

FAMILY ABROCOMIDAE MILLER AND GIDLEY, 1918

The family includes one living genus, *Abrocoma,* and the extinct genus *Protabrocoma* Kraglievich, 1927.

Diagnostic characteristics of the Abrocomidae presented by Ellerman (1940) and Woods (1984) include some that may be synapomorphic for the family. Others are not unique, although they are present in all members of the family and each character serves to distinguish the family from some other group or groups. Among the characteristics cited by Ellerman and Woods are: body size small; upper cheekteeth with simplified occlusal pattern that is "eight-shaped" (fig. 1); lower cheekteeth distinctly different in pattern (fig. 9); jugal process variable; paroccipital process short and fused to bulla; coronoid process of dentary reduced (fig. 10); lacrimal canal open on rostrum near dorsal root of zygoma (fig. 5); palatal foramina long and narrow; zygoma delicate (fig. 8); angular process of dentary delicate and close to axis of alveolus of incisor (that is, subhystricognathous). Some of these characters are clearly parts of larger related complexes of characters.

Waterhouse (1837: 32) in his original description of *Abrocoma* noted that "The genus *Abrocoma* is evidently allied on the one hand to *Octodon, Ctenomys,* and *Poephagomys* [= *Spalacopus*], and it appears to be almost as evidently allied on the other hand, to the Chinchillidae."

Ellerman (1940) mentioned that *Abrocoma* "is reminiscent of the Chinchillidae" in the length and narrowness of the palatal [= incisive] foramina and that the stiff bristle hairs on central digits are "as in Chinchillidae and

Fig. 9.   Left upper (at left) and left lower (at right) molariform tooth rows of *Abrocoma* n. sp. (MVZ 120238). Scale represents 1 mm.

Octodontidae." Others (Miller and Gidley, 1918; K. F. Koopman, personal commun.) have allied the Abrocomidae to the Chinchilloidea instead of the Octodontoidea. Miller and Gidley distinguished a "Group B" on the basis of partly open lacrimal canal (fig. 5) and large lacrimal bone. This group included *Dasyprocta,* as well as Chinchillidae and Abrocomidae. Landry (1957: 50–51) also commented on some of the above similarities of *Abrocoma* and *Chinchilla.*

Abrocomidae were tallied by Hartenberger (1984: 27) as resembling Octodontidae in lacking "cement on molar crown." In contrast, cement was tallied as present in Chinchillidae, Caviidae, and Hydrochaeridae. However, the term "cement on molar crown" is cryptic, and his scoring is incorrect and needs revision. For example, the holotype of *Abrocoma* n. sp. (BM 34.9.2.171, fig. 1A) has cement in each reentrant enamel fold (lingual and labial, upper and lower of all molariform

teeth) and this cement is exposed on the flat occlusal surface. The surface of this cement is slightly lower than that of the harder adjacent enamel layer, but is clearly undergoing wear at the occlusal surface. In the smaller of the two specimens of *Abrocoma* n. sp. and in most specimens of other species of *Abrocoma* there is less occlusal exposure of cement, either because less cement is present in the reentrant angles or wear keeps the surface of the cement well below the level of enamel and dentine. In all cases, however, the reentrant angles are largely filled with cement. When the cement does not reach the occlusal plane it is not clear to what degree this results from greater wear of the softer cement and to what degree growth of the continually emerging tooth has not proceeded far enough to bring the cement to the surface.

The presence of occlusally exposed cement is no more prevalent in Caviidae than in Octodontidae. *Cavia* has a conspicuous expo-
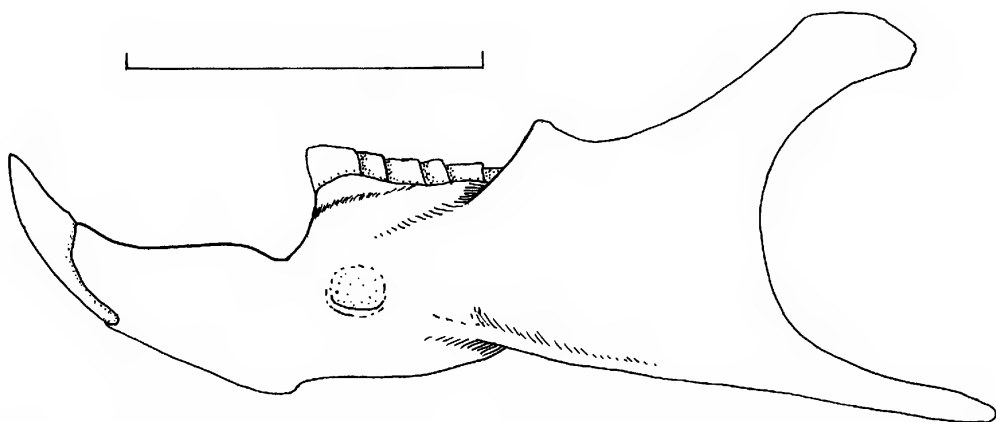
Fig. 10. Side view of mandible of *Abrocoma* n. sp. (BM 34.9.2.171). Scale represents 10 mm.

sure of cement (fig. 1G) but there is little in *Galea* or in *Microcavia* (fig. 1H). Cement is generally exposed occlusally in those genera of Octodontidae that retain reentrant angles (as shown in fig. 1C, D, E) although to a lesser degree than in *Abrocoma* (fig. 1A) or in Chinchillidae (fig. 1B).

Among Octodontidae, occlusal cement is apparent in *Aconaemys* (fig. 1C), *Octodon* (fig. 1D), and *Spalacopus* (fig. 1E), although it is not evident in *Octodontomys* (fig. 1F). *Octodontomys* and *Ctenomys* (fig. 1I), have simplified teeth that lack reentrant angles and cement.

The Chinchillidae are distinctive in the formation of their transverse lophs (fig. 1B). The posterior enamel layer is reduced or lost, cement extends into this area as a lamina completely bridging the tooth, and the laminae are closely appressed.

Genus *Abrocoma* Waterhouse, 1837

Abrocoma Waterhouse, 1837: 30, type species *A. bennetti* by original designation.
Habrocoma Wagner, 1842: 288, invalid emendation of *Abrocoma*.

Characters that we regard as synapomorphies for *Abrocoma* (and hence diagnostic in a more restricted cladistic sense than in the traditional usage reflected above) are:

1. Number of folds on lower cheekteeth increased to one labial and two deep lingual folds on each of the four teeth (fig. 9). This assumes that the primitive number of folds was fewer than this number in this lineage.

These dental features were the main basis for Waterhouse's recognition of the genus in 1837.

2. Zygomatic arch delicate; anterior ascending process of maxilla reduced to a slender strut (fig. 8); jugal part of this dorsal zygomatic bridge reduced to the ventral base of the bridge and thus jugal well separated from lacrimal; no posterior projection of jugal beyond general curvature at the back of the arch.

3. Loss of a ventral groove (behind a bony plate) in medioventral border of infraorbital canal (fig. 11). The presence of some sort of a plate or ridge separating, completely or partly, a canal or trough is presumed to be plesiomorphic at level 1 of figure 4. The condition occurs in various genera of Echimyidae (one example is shown in fig. 11; we have not looked at all genera), and tends to be reduced or lost when the basal capsules of lengthened molariform or incisor teeth encroach on the area (for example, in most *Ctenomys* and in *Lagidium* and *Chinchilla* of the Chinchillidae, as well as in *Abrocoma*). Among octodontids other than *Octodontomys* (shown in fig. 11), this flange is higher in *Octodon* and is encroached upon and reduced by the backwardly extending incisor capsule in *Aconaemys* and even more so in *Spalacopus,* but both canal and flange are present. (Also, they may be absent in *Tympanoctomys*; L. Contreras, personal commun.)

4. Rostrum narrowed, including nasals, premaxillaries, and maxillaries, incisive fo-
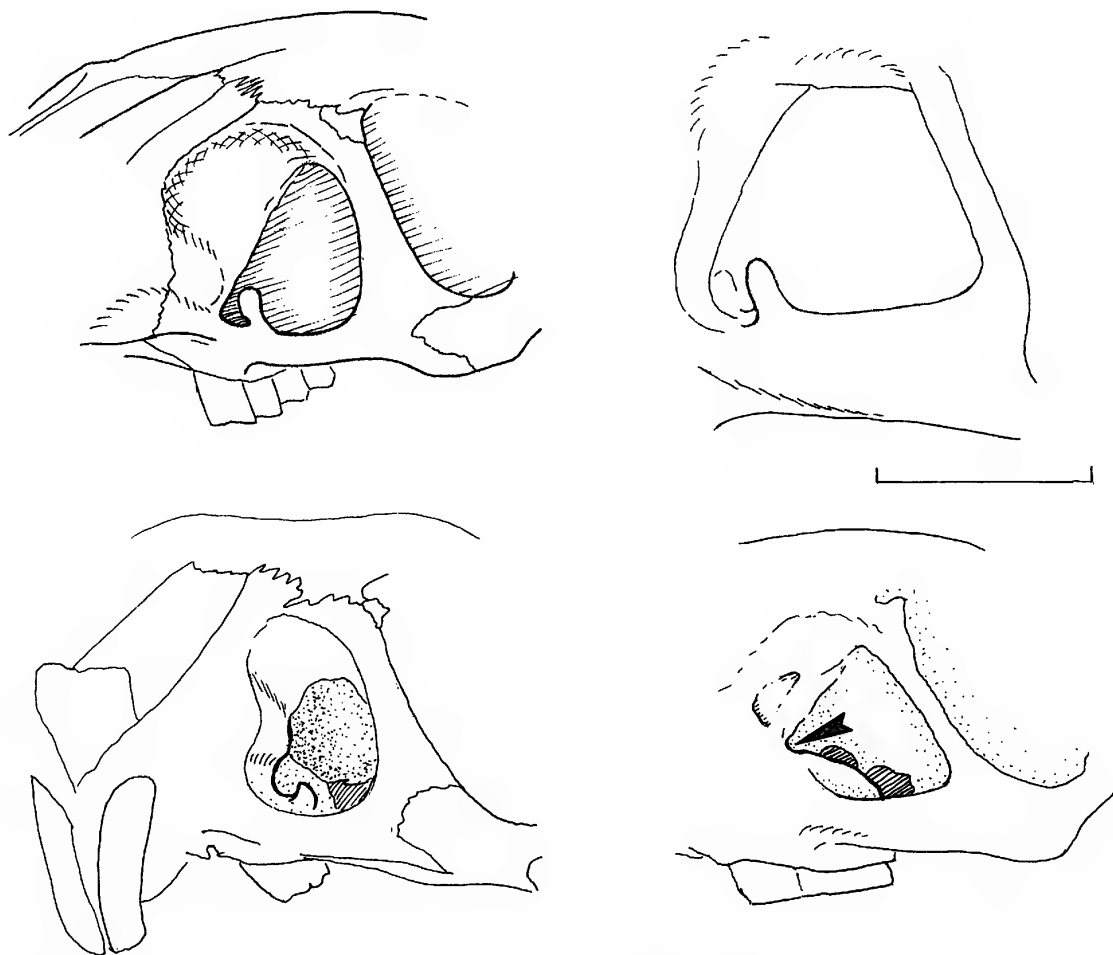
Fig. 11. Anterolateral view of infraorbital canal showing ventral bony flange shielding a canal, presumably for passage of nerve, in an octodontid (*Octodontomys gliroides,* upper left, AMNH 249052), in a chinchillid (*Lagostomus maximus,* upper right, AMNH 262287), in an echimyid (*Thrichomys apereoides,* lower left, AMNH 260860), and the encroachment from below of the capsule for the roots of high crowned molariform teeth, the absence of a flange, and the reduction of the nerve canal to a shallow groove (arrow) in *Abrocoma* (lower right, MVZ 120238). Scale represents 10 mm.

ramina, and incisors. Incisors are also shortened. These features occur also in *Chinchilla* and *Lagidium* but to a lesser degree.

5. Lower incisors and anterior part of dentaries narrowed. Incisors also shortened, foramen leading to base of incisor capsule lies in trough ventrolateral to the posterior molar (more or less as in *Chinchilla* and *Lagostomus,* in *Lagidium* the foramen is actually slightly medial to the axis of the tooth row) rather than dorsolaterally about halfway between the tooth and the tip of the articular process, as in octodontids.

6. Angular process narrowed, elongated, and turned medially to a subhystricognath

position. Thus semilunar notch widened (fig. 10). These features occur also in *Chinchilla* and *Lagidium* but to a lesser degree.

7. Coronoid process reduced (fig. 10). This feature occurs also in *Chinchilla* and *Lagidium* but to a lesser degree.

8. Bullae enlarged, mastoids appear dorsally on skull between parietal, squamosal, and occipital bones (fig. 12); lateral processes of supraoccipital correspondingly reduced. These features occur also in *Chinchilla* and *Lagidium* but to a lesser degree.

9. Feet reduced in length and width. Toes and claws shortened (fig. 13).

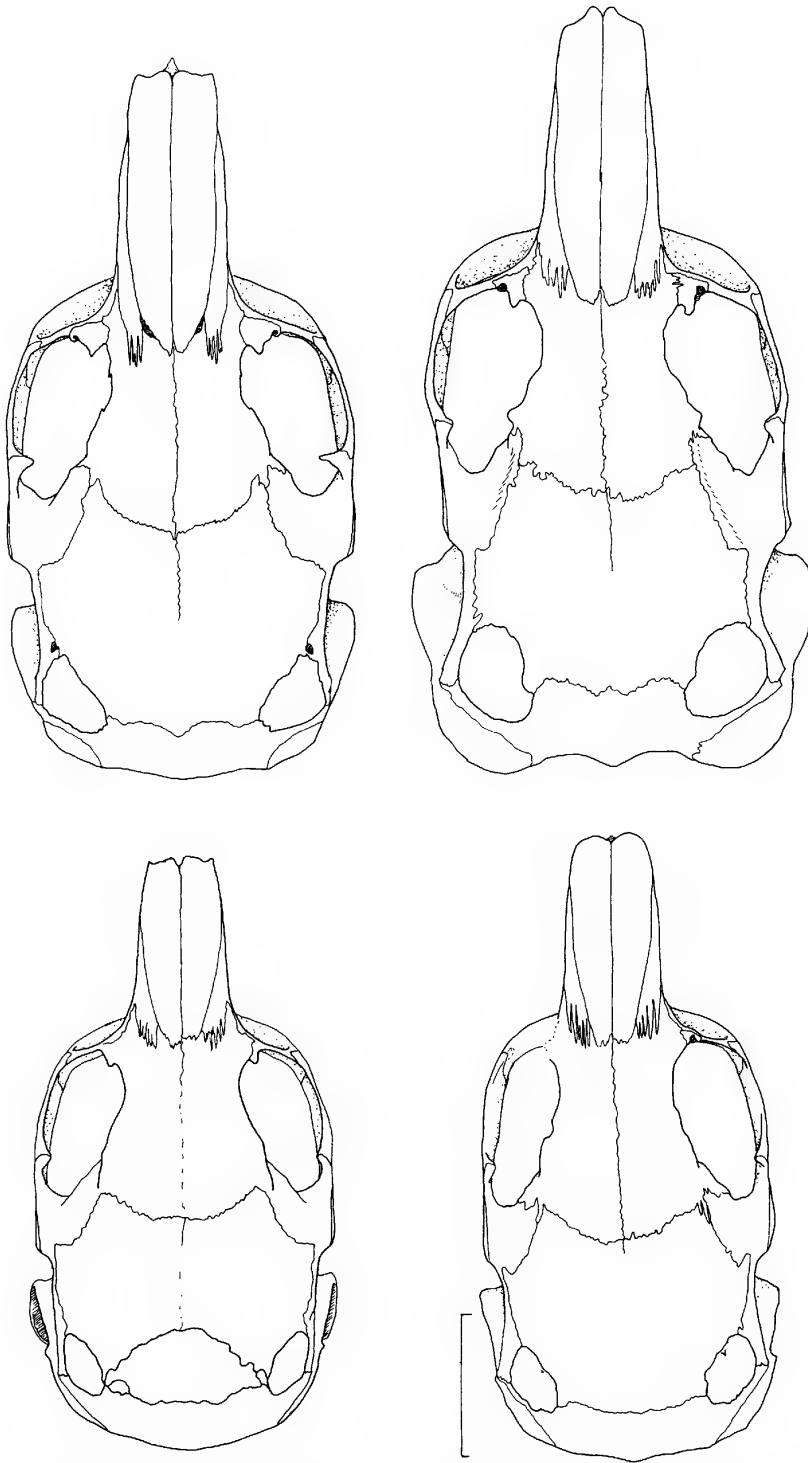10. Pedal digit 2 specialized, with wide,

Fig. 12.   Drawings of dorsal views of skulls of *A. bennetti* (upper left, MVZ 150117), *A. cinerea* (upper right, MVZ 116803), and *Abrocoma* n. sp. (lower left, MVZ 120238; and lower right, holotype, BM 34.9.2.171). Scale represents 10 mm.
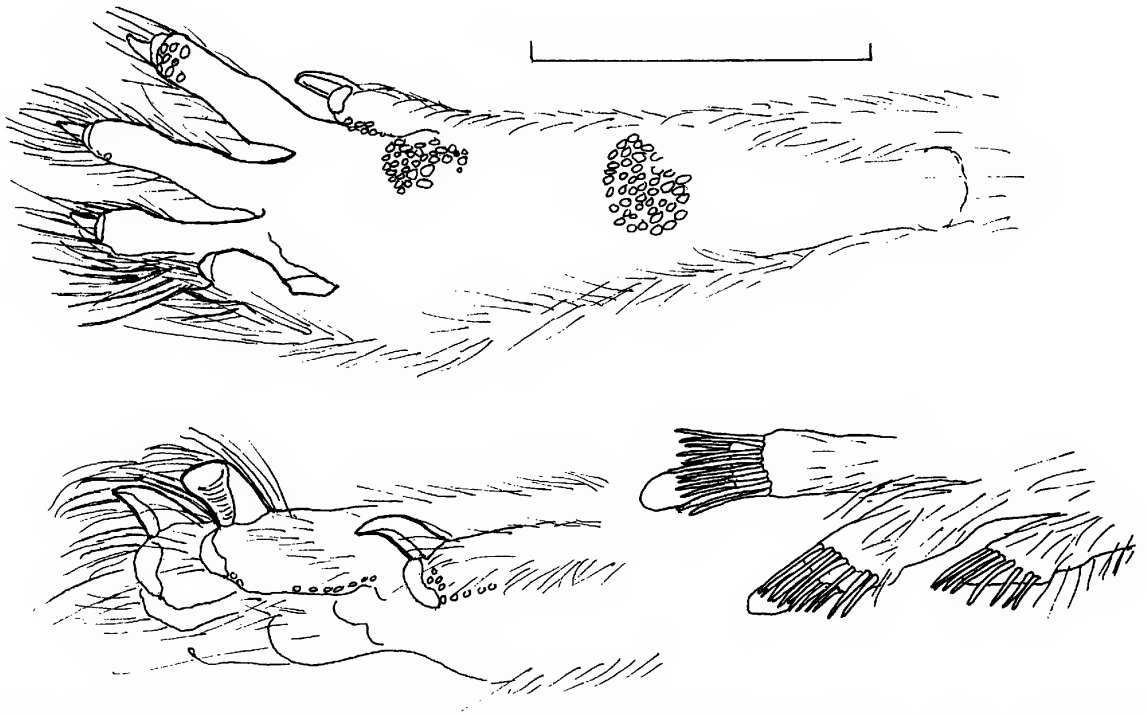
Fig. 13.   Drawings of right hind foot of *Abrocoma* n. sp. (MVZ 120238), ventral view above; side view of D1 to D3, below at left; and mediolateral view of D1 to D3 of *Ctenomys frater mordosus* (AMNH 263014) to show fully developed ctenodactyloid combs, at lower right. The size and spacing of tubercles are shown on sample areas. These tubercles occur over the entire palmar surface. Scale represents 10 mm.

distally rounded, ventrally hollowed claw, with slight groove lateral to the claw, and with well-developed "ctenodactyloid" row of stiff hairs above the claw. This hair-comb also present on digits 3 and 4, but less well developed. The postulated evolutionary development proceeds from relatively uniform short hairs on foot and toes, to lengthening and thickening of hairs on distal part of toes, then certain of these hairs thicken further basally and form in a distinct row just above the claw. In *Ctenomys* more than one (usually two, rarely the beginnings of a third) distinct row of such hairs are present on some digits, generally D2 to D4. In other genera, the overall development of combs is less than in *Ctenomys,* the degree of development is less on the lateral digits than on the central three digits, and of these generally most developed on D2.

11. Palmar surfaces of feet and bottoms of toes unhaired and covered with small, distinct tubercles (noted by Waterhouse, 1837), except for a larger terminal pad beneath each claw (shown in fig. 13). The numerous small tubercles are probably about as high as wide in life (we have not examined this closely in living animals) and presumably function to increase friction, perhaps with rock surfaces or branches of trees.

12. Tendency to form a single medial foramen in palate halfway between incisive foramina and mesopterygoid fossa (see Ellerman, 1940: 152). This is present in at least some skulls in each of the three species.

Other characteristics of the genus are:

1. Size smaller than in many other caviomorph rodents (such as Hydrochaeridae, Agoutidae, Dasyproctidae, Erethizontidae, Capromyidae, Myocastoridae, Hystricidae, some Caviidae, and most Chinchillidae), but comparable to some members of the families Octodontidae and Ctenomyidae.

2. Upper cheekteeth simplified, somewhat as in Octodontidae and Ctenomyidae.

3. Paroccipital process short and fused to bulla, as in Octodontidae and Ctenomyidae; not elongate and distally free as in some other

caviomorph families (e.g., Myocastoridae, Capromyidae, Hystricidae, and Agoutidae). Other groups display intermediate conditions of length, closeness to bulla, and degree of fusion with bulla.

4. Ears relatively large and rounded, although a concavity of the posterior margin of the pinna is present as in most caviomorphs.

5. Lower jaw without ridge or groove on lateral surface (these are present in the Caviidae and Hydrochaeridae; Lawlor, 1979).

6. Upper toothrows more or less parallel (these converge anteriorly to various degrees in some other families, most extremely in Caviidae, where the alveoli of anterior molariform teeth may meet).

KEY TO RECENT SPECIES OF *ABROCOMA*

1. Larger, occipitonasal length of skull more than 55 mm; zygomatic arch, especially the anterior bridge to lacrimal, heavy; rostrum heavier, sides distinctly divergent posteriorly; interorbital area relatively less constricted; angular process of mandible not so slender. Peru. No living population discovered. (fig. 14) .... *Abrocoma oblativa*

Smaller, occipitonasal length of skull less than 55 mm; zygomatic arch relatively slender, especially the anterior bridge reduced to a thin strut; rostrum relatively slender and parallel sided; interorbital constriction greater; angular process slender (fig. 8); known only from south of 15° latitude in southern Peru (fig. 15) 2

2. Tail less than 60% of length of head and body; dorsal pelage pale gray (fig. 16); bullae especially large (fig. 17), bullar width of skull exceeding zygomatic width by more than 2 mm .... *Abrocoma cinerea*

Tail more than 60% length of head and body; dorsal pelage darker gray; bullar width about the same as zygomatic width 3

3. Tail hairier (fig. 18), distal third with many hairs more than 5 mm long; ventral pelage whitish to pale gray at tips, in some areas white to base of hairs (fig. 19); feet whitish above, and relatively unpigmented below; occipitonasal length of skull less than 42 mm .... *Abrocoma* n. sp.

Tail less hairy, distal third with few if any hairs longer than 3 mm; ventral pelage pale gray-
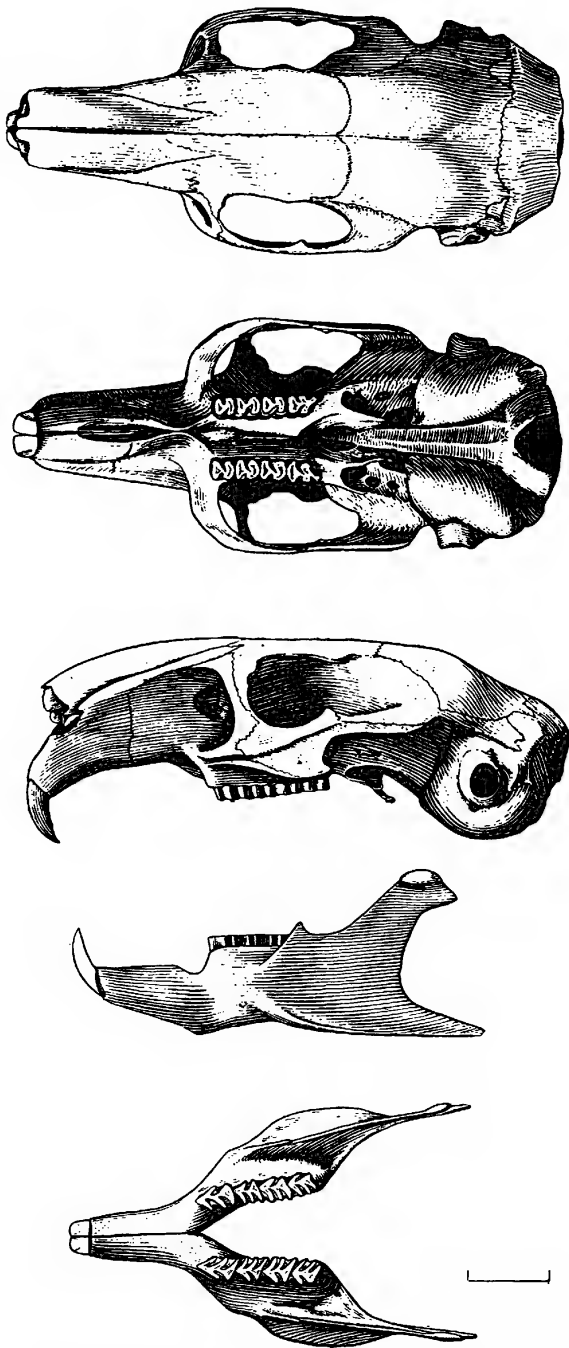

Fig. 14.　Skull drawings of *Abrocoma oblativa* (from Eaton, 1916). Scale represents 10 mm.

ish, hairs generally darker at the base, no patches of white; feet darker, grayish hair above and blackish plantar surfaces; occipitonasal length of skull more than 42 mm·· .... *Abrocoma bennetti*
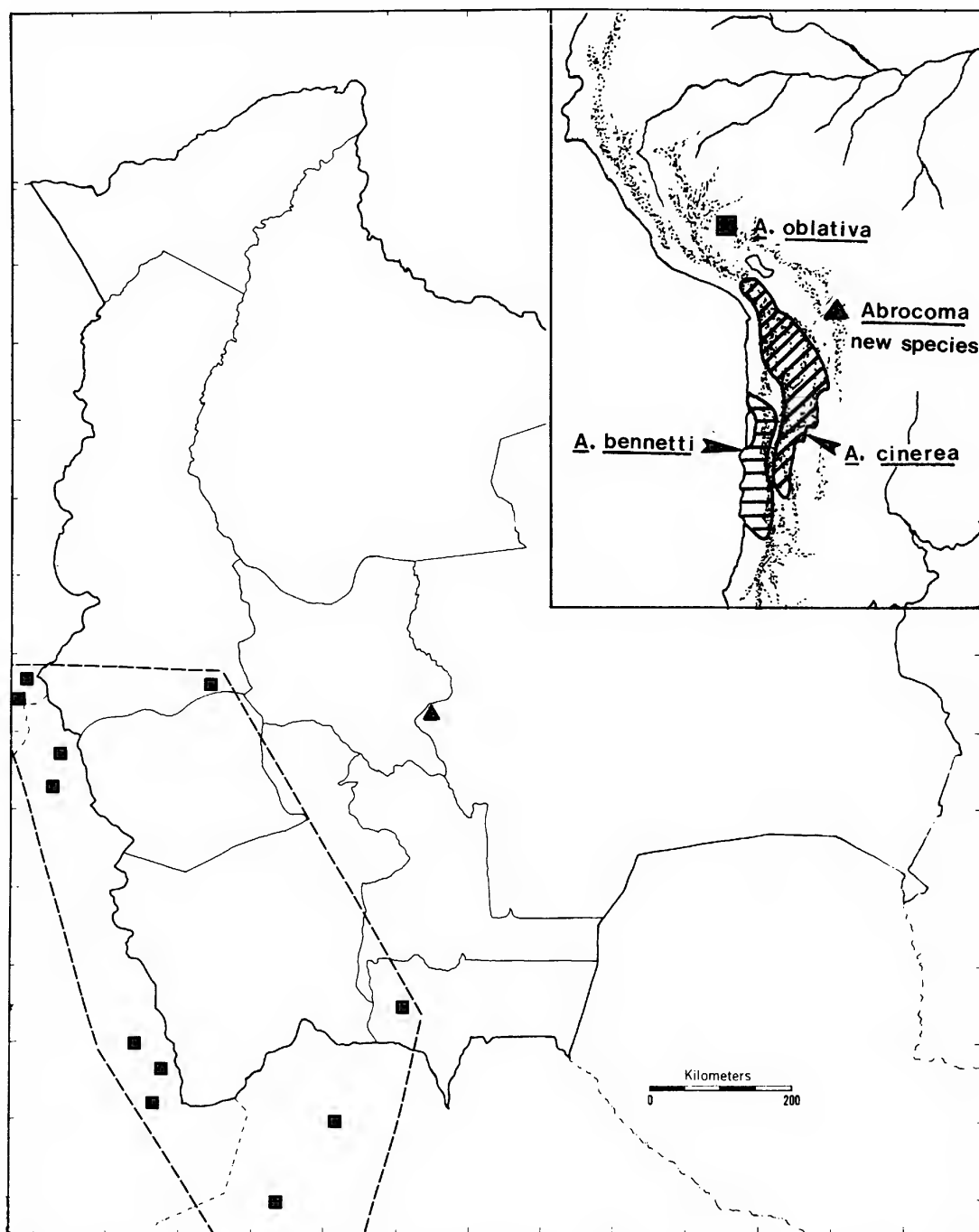
Fig. 15. Map of Bolivia and environs showing *Abrocoma* localities: *A. cinerea* (squares), *A.* n. sp. (triangle). Inset map of west-central South America showing distribution, as now known, of *Abrocoma*.

The ratio diagram in figure 20 (and data in tables 1 and 2 on which fig. 20 is based) illustrates most of the differences in size and proportions that are mentioned in the key and in the comparisons below. Externally, the short ears and long tail (relative to the length of head and body) of the new species are clear. Cranially, enlargement of auditory bullae (BUL, BUW, and BBW) is seen to be greatest (relative to CBL) in *A. cinerea*; and *A. bennetti murrayi* has bullae that are intermediate in size between those of *A. cinerea* and the
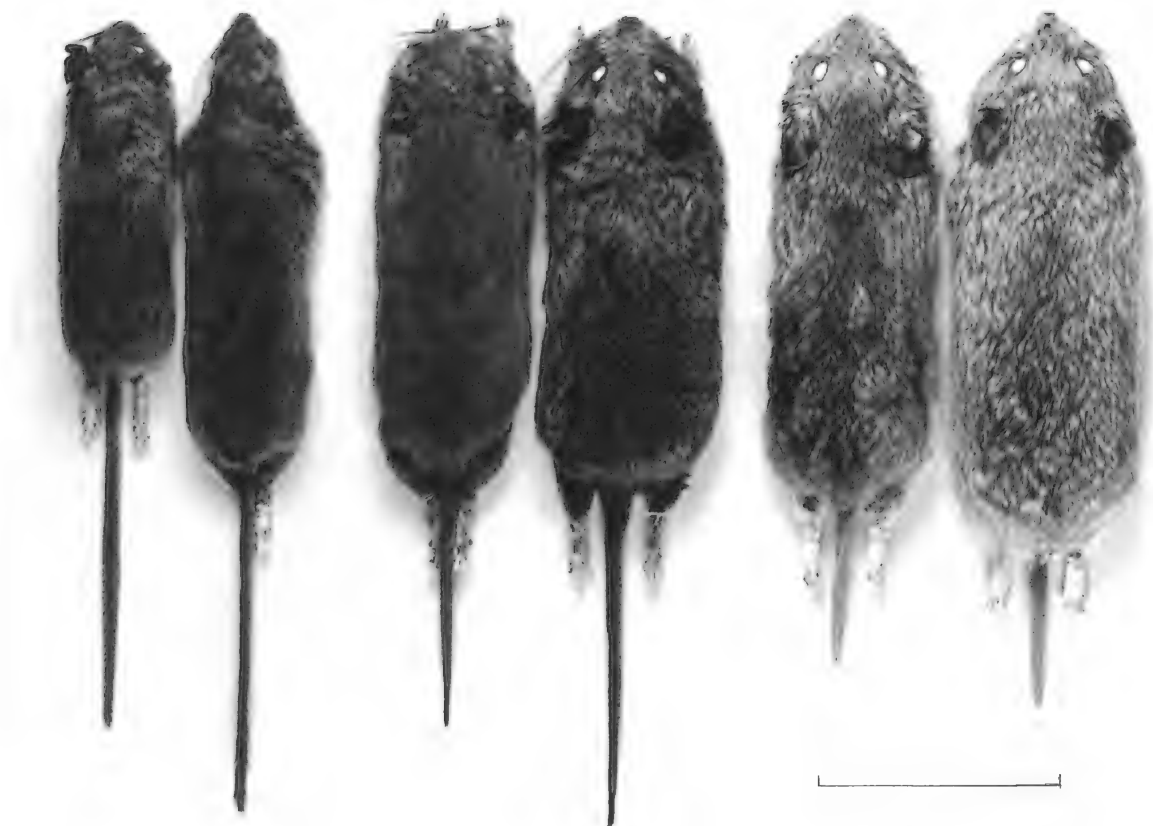
Fig. 16. Study skins in dorsal view (from left to right) of *Abrocoma* n. sp. (MVZ 120238 and BM 34.9.2.171), *A. bennetti* (AMNH 33273 and MVZ 118669), and *A. cinerea* (MVZ 116803 and MVZ 116801). Scale represents 100 mm.

smaller bullae of *A. bennetti bennetti*. The new species has relatively smaller bullae than *A. cinerea* or *A. bennetti* have, but relatively larger than *A. oblativa* has. Furthermore, the proportions of the bulla itself are different in the new species which has a relatively longer bony meatal tube (as shown by the much smaller bullar bulb, BBW, as compared to the total width of the bullae with the meatal tube included, BUW). The relatively small bullae, as noted, and relatively wide inter-orbital area (IOB/CBL) of *A. oblativa* are conspicuous.

A fifth species of *Abrocoma, A. antiqua* Rovereto, is known from the Huayquerias, Mendoza Province; and Huayquerian, Chiquimil, Catamarca Province, in Argentina (Spencer, 1987; see Marshall and Patterson, 1981, for summary of the geochronology of the Catamarca sites, which place the Hu-

ayquerian at about 6 million years of age and comparable to the late Miocene of North America). The length of the molariform series of teeth in the dentary of *A. antiqua* was given as 11.5 mm (Rovereto, 1914: 67) which indicates a larger size than species known to be living (*A. bennetti, A. cinerea,* and the new species here described) and smaller than *A. oblativa,* which may or may not be living in Perú. The upper teeth figured by Rovereto were said (by Spencer, 1987) to have been incorrectly associated with the lower teeth of the holotype.

Abrocoma boliviensis, new species

HOLOTYPE: 34.9.2.171, BM(NH); skin and skull; female; obtained by F. B. Steinbach, field number 26, on 14 October 1926.

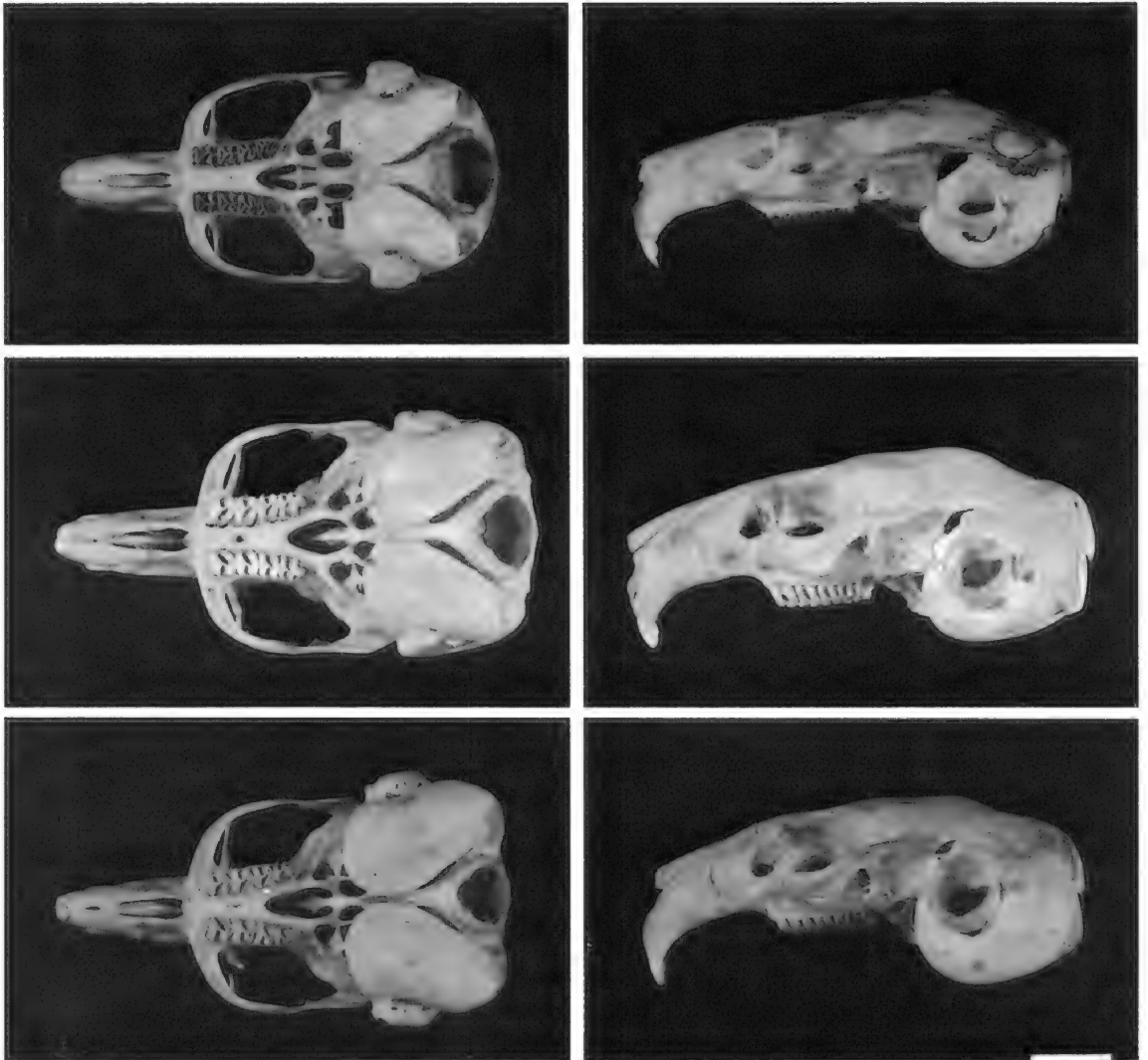OTHER SPECIMENS: One from 5 mi (= 8 km)

Fig. 17. Ventral and lateral views of skulls of *Abrocoma* n. sp. (MVZ 120238, top), *A. bennetti* (AMNH 33273, middle), and *A. cinerea* (MVZ 116006, bottom). Scale at lower right represents 10 mm.

by road west of Comarapa, collected by O. P. Pearson, field number 4186, on 13 September 1955.

TYPE LOCALITY: Comarapa, "2500 m," province of Manual M. Caballero, department of Santa Cruz, Bolivia; 17°54′S and 64°29′W. Since Comarapa is at 1815 m (Atlas Censal de Bolivia), some uncertainty about the exact place of origin exists. The terrain reaches 2500 m within a few kilometers to the north, west, and south of the town of Comarapa.

DISTRIBUTION: Known only from the type locality or nearby.

DIAGNOSIS: An *Abrocoma* distinguishable from *A. cinerea* by darker dorsal and ventral pelage; dorsal hair shorter and not so soft; much longer and hairier tail; relatively smaller head; smaller size; smaller bullae; relatively shorter nasals, not extending posterior to anterior edge of orbit; and jugal slightly narrower (see fig. 20 for these and other ratios).

Distinguishable from *A. bennetti* by usually longer and always hairier tail; ventral color paler and hairs of some irregular ventral areas white to roots, unlike gray roots in *A. bennetti*; tops of feet paler; plantar surfaces of feet less pigmented; feet smaller; relatively smaller and narrower head; relatively wider

Fig. 18. Distal part of tail to show longer hairier tail in the new species and shorter paler tail in *Abrocoma cinerea* (left to right, *Abrocoma* n. sp. (BM 34.9.2.171) *A. bennetti* (MVZ 118669), and *A. cinerea* (MVZ 116801). Scale represents 10 mm.

foramen magnum; bullae smaller; relatively shorter nasals, not extending posterior to anterior edge of orbit; and jugal much narrower.

Distinguishable from *A. oblativa* (known from skeletal material only) by smaller size; tooth rows more divergent posteriorly; bullae larger and with greater areas of exposure on dorsal surface of skull; zygomatic arch more slender, especially the anterior bridge to the lacrimal area; rostrum more slender both from side to side and top to bottom.

Among living *Abrocoma* species, *A. boliviensis* is most similar to *A. bennetti* in general appearance, especially in its dark dorsal coloration and relatively long tail. These species, and *A. oblativa* whose external features are unknown, also have relatively smaller bullae than does *A. cinerea* (fig. 19). It is interesting to note that geographic variation in bullar size occurs within *A. bennetti*. Two subspecies, *A. b. bennetti* and *A. b. murrayi*, are distinguished (Osgood, 1943). The latter subspecies, although closest geographically to *A. boliviensis*, has proportionately larger bullae than the more distant *A. b. bennetti* (see fig. 19 and table 2). The small bullae of *A. boliviensis* and *A. b. bennetti* may reflect adaptation to similar, densely vegetated habitat (see Osgood, 1943, and Habitat section below) in contrast to the sparsely vegetated desert habitat occupied by *A. b. murrayi* and arid altiplano habitat of *A. cinerea*.

Fig. 19. Ventral view (same specimens as in fig. 16) to show white areas on venter of *Abrocoma* n. sp. and paler venter in *A. cinerea* than in *A. bennetti*. Scale represents 100 mm.

HABITAT: The habitat of the specimen captured by O. P. Pearson was described by him in 1955 as brushy vegetation with patches of cloud forest, and the Comarapa river valley below was similar but more cultivated. Traps were set "along a ridge with rock outcrops plus bushes, grass, and many succulents, plus a few orchids . . . and ferns." A few traps were set in the cloud forest. The *Abrocoma* was taken on the ridge. In 1984 and 1987, visits to the area (by Anderson) revealed a general similarity to Pearson's description and photographs in his notes, however the intensity of human use was clearly greater. No nearby cloud forest was evident and few succulents or ferns. The area was heavily grazed by livestock. Little grass was to be seen. Trees were fewer and smaller. There were cultivated areas on the hillsides as well as in the valley below.

Both *Abrocoma bennetti* and *A. cinerea* are highly herbivorous (Pearson, 1951; Koford, 1955; Glanz and Meserve, 1982; Meserve et al., 1983), feeding primarily on shrub leaves, buds, and bark; these preferences may account for their reluctance to come to baited traps (Pearson, 1951; Koford, 1955; Glanz, unpublished). If *A. boliviensis* has a similar diet, obtaining additional specimens may require considerable effort. New trapping techniques and collecting at additional localities in the diverse "valles" region of central Bolivia are needed also.

ETYMOLOGY: The name indicates the species' occurrence in Bolivia.

CONCLUDING COMMENTS

The two known specimens of the new species of *Abrocoma* were obtained by a general collector (Franz Steinbach in 1926) and a mammalogist (O. P. Pearson in 1955) who
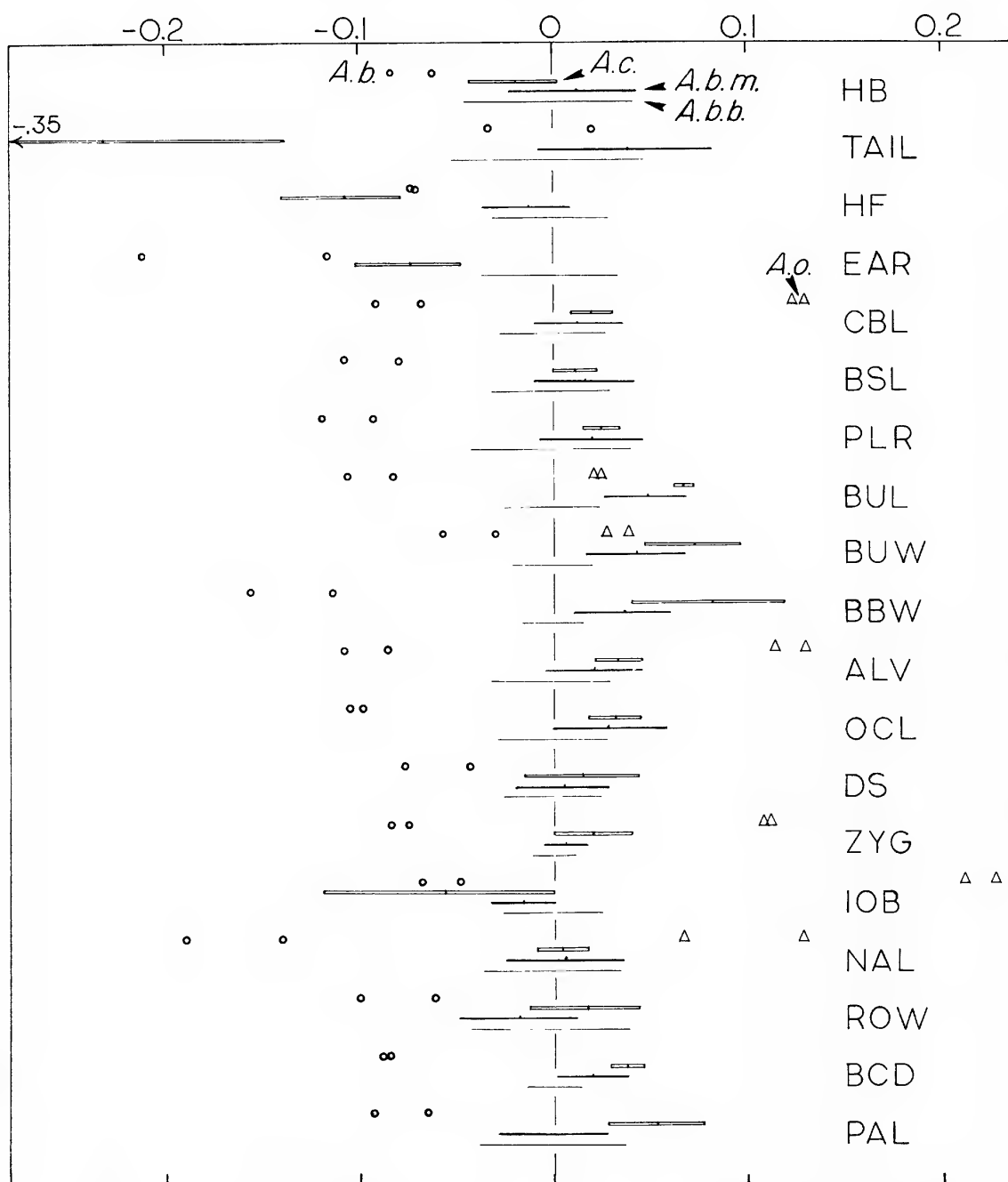
Fig. 20. Ratio diagram to show relative proportions of external and cranial dimensions (log differences on abscissa) graphed for 19 measurements of five taxa of *Abrocoma*: *A.b.* = *A. boliviensis*, *A.c.* = *A. cinerea*, *A.b.b.* = *A. bennetti bennetti*, *A.b.m.* = *A. bennetti murrayi*, and *A.o.* = *A. oblativa*. Ranges shown represent one standard deviation on either side of the mean. Dimensions measured are noted under Methods. Specimens are listed in the Appendix.

was seeking information on a genus of rodents (*Phyllotis*) in a different family. Recently we recognized the identity and the specific uniqueness of these two specimens as

parts of studies devoted to other objectives, namely field studies of rodent ecology in Chile (Glanz) and a general survey of Bolivian mammals (Anderson). In attempting to learn

TABLE 2

Cranial Measurements (in millimeters) of *Abrocoma*

(Mean and standard deviation are given for each dimension with the minimum and maximum measurements in parentheses)

Variable	A. bennetti bennetti	A. bennetti murrayi	A. cinerea (all subsp.)	Abrocoma oblativa[a]	Abrocoma boliviensis
N	12	12	5	2	2
Condylobasal length	48.1 ± 3.0 (42.1–52.8)	49.6 ± 2.5 (46.0–54.1)	50.4 ± 1.2 (48.4–51.4)	64.4 (63.8–65.0)	40.1 (39.0–41.1)
Modified basal length	42.3 ± 3.0 (36.4–46.7)	44.0 ± 2.6 (38.9–48.2)	43.4 ± 1.1 (43.2–45.8)	—	34.1 (32.9–35.2)
Palatilar length	25.5 ± 2.4 (20.8–29.4)	26.7 ± 1.6 (24.1–29.8)	27.0 ± 0.6 (26.4–27.9)	—	19.9 (19.3–20.5)
Bullar length	14.3 ± 0.8 (13.5–16.0)	16.0 ± 0.8 (14.8–17.1)	16.7 ± 0.2 (16.5–17.0)	15.0 (15.0)	11.5 (11.2–11.8)
Bullar width	10.5 ± 0.5 (9.8–11.3)	11.6 ± 0.7 (10.4–12.6)	12.4 ± 0.7 (11.8–13.6)	11.4 (11.2–11.5)	9.5 (9.2–9.8)
Bullar bulb width	8.2 ± 0.3 (7.8–8.6)	8.9 ± 0.5 (8.1–9.8)	9.9 ± 0.9 (8.7–11.0)	—	6.0 (5.7–6.3)
Alveolar length	10.0 ± 0.7 (8.8–10.9)	10.5 ± 0.6 (9.6–11.2)	10.8 ± 0.3 (10.6–11.3)	13.3 (13.0–13.5)	8.0 (7.8–8.2)
Occlusal length	9.3 ± 0.6 (8.1–10.1)	9.9 ± 0.6 (8.8–10.6)	10.0 ± 0.3 (9.7–10.5)	—	7.4 (7.3–7.4)
Dental span	8.6 ± 0.5 (7.5–9.2)	8.7 ± 0.5 (8.0–9.4)	8.9 ± 0.6 (8.1–9.3)	—	7.5 (7.2–7.8)
Zygomatic breadth	22.6 ± 1.2 (20.4–24.5)	22.9 ± 0.6 (21.8–23.5)	23.7 ± 1.1 (22.6–24.9)	29.1 (29.0–29.2)	18.8 (18.6–19.0)
Interorbital breadth	8.3 ± 0.5 (7.7–9.3)	8.0 ± 0.3 (7.6–8.7)	7.3 ± 1.0 (6.2–8.3)	13.8 (13.5–14.0)	7.3 (7.1–7.4)
Length of nasals	19.7 ± 1.6 (17.2–22.8)	20.0 ± 1.4 (17.2–22.5)	19.9 ± 0.6 (18.9–20.4)	24.8 (23.0–26.5)	13.6 (12.7–14.4)
Width of rostrum	7.5 ± 0.7 (6.5–8.5)	7.2 ± 0.5 (6.4–8.2)	7.8 ± 0.5 (7.1–8.3)	—	6.2 (5.9–6.5)
Braincase depth	18.4 ± 0.6 (17.8–19.8)	19.3 ± 0.8 (18.1–20.4)	20.1 ± 0.4 (19.6–20.7)	—	15.1 (15.0–15.1)
Length of palate	9.3 ± 0.8 (8.1–10.4)	9.3 ± 0.6 (8.4–10.0)	10.5 ± 0.6 (9.6–11.1)	—	7.8 (7.5–8.0)

[a] Measurements taken or calculated from Eaton (1916).

more about the newly discovered *Abrocoma boliviensis* in the field we (Anderson and associates) obtained the first specimens of two other species new to science, *Oxymycterus hucucha* (Hinojosa et al., 1987) and *Akodon siberiae* (Myers and Patton, 1989). Thus a chain of serendipitous discoveries continues. The unifying theme or scientific objective has been simply to learn more about our universe and more specifically about biodiversity in the Neotropics. This remains a valid, timely, exciting, and productive objective. We would

not have ventured into the problems of family-level classification of caviomorph rodents except out of curiosity about the relationships of our new species of *Abrocoma*.

The controversial relationships outlined (in fig. 4) contrast with other postulated phylogenies, for example, with Woods' (1984: 410) "consideration of the superfamily Chinchilloidea as one of the ancient lineages of the New World Hysticognathi with no really close affinities with other New World families." The phylogeny of figure 4 is quite tentative;

however, so are the various contrasting phylogenies at this point.

Since there is no consensus as to what a classification should accomplish or as to which of several sometimes conflicting goals is paramount, it is especially important that each revisor indicate the premises and goals of each classification presented. At this stage, it seems both unnecessary and undesirable to modify the formal classification with each new interpretation (a view expressed earlier by Anderson, 1974). Hopefully, an eventual convergence of views will allow the classification to be revised with prospects for relatively greater stability.

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APPENDIX

Specimens referred to in text, noted in legends to figures, or measured for data in tables (arranged alphabetically by genus and species) are:

Abrocoma bennetti bennetti. CHILE. Province of Santiago; Fundo Santa Laura, 10 km W of Tiltil, 1000 m (150117 MVZ). Province of Valparaiso, Quilpue (33273 AMNH). Province of Coquimbo, Fray Jorge, 310 m (118669 MVZ). Specimens used for tables were: CHILE, 13. Province of Coquimbo; Fray Jorge (118668, 118669 MVZ). Locality noted above (150117 MVZ). Province of Valparaiso; Banos de Cauquenes (23148 FMNH); Limache (283917 USNM); Olmue (23149–23153 FMNH); Papudo (23209 FMNH); Quilpue (33273, 33274 AMNH).

Abrocoma bennetti murrayi. Specimens used for tables were: CHILE, 12. Province of Coquimbo; Domeyko (23172 FMNH); Romero (23154–23163 FMNH and 259640 USNM); Vallenar (23169, 23170 FMNH).

Abrocoma boliviensis. Specimens used in text and in tables were: BOLIVIA, 2. Department of Santa Cruz; Comarapa (34.9.2.171, holotype, BM); 5 mi (8 km) W of Comarapa, 7500 ft (2320 m; 120238 MVZ).

Abrocoma cinerea. PERU. Department of Tacna; 2 km N of Nevado Livine, 4170 m (116006 MVZ). CHILE. Province of Antofagasta, Toconce, 60 km ENE of Calama, 4320 m (116801 and 116803 MVZ); Province of Santiago, 10 km W of Tiltil, 1000 m (150117 MVZ). Specimens used for tables were: ARGENTINA, 3. Province of Catamarca; Cerro Ambato (23641 USNM). Province of Salta; Chorrillos, Los Andes (35239 USNM). Province of San Juan; Los Sombreros, Sierra Tontal (46157 USNM). CHILE, 5. Province of Antofagasta; San Pedro (116805 MVZ); Toconce (116801–116804 MVZ). PERU, 3. Department of Puno; Caccachara (116005 MVZ). Department of Tacna; Challapalca (141626 MVZ); Nevado Livine (116006 MVZ).

Abrocoma oblativa. Measurements are from Eaton (1916: 88) for Yale University Osteological Collection nos. 3318 and 3320, from Machu Picchu, Department of Cuzco, Peru.

Aconaemys fuscus. CHILE. Province of Nahuelbuta; Araucaria Forest, 1140 m (91655 AMNH).

Cavia aperea. BOLIVIA. Department of Santa Cruz; Estancia Cachuela Esperanza, 300 m (260799 AMNH). LABORATORY (149996 AMNH).

Chinchilla lanigera. Bred in captivity (148463, 148465 AMNH).

Coendou bicolor simonsi. BOLIVIA. Department of Cochabamba, Palos Blancos, Alto Beni (262273 AMNH).

Coendou mexicanus. NICARAGUA. Matagalpa (28339 AMNH).

Coendou prehensilis. ZOO SPECIMEN (130368 AMNH).

Ctenomys frater mordosus. BOLIVIA. Department of Tarija; 8 km W of Rancho Tambo, 2700 m (263011 AMNH).

Erethizon dorsatum. IDAHO. Fremont County, N. fork Snake River (120848 AMNH).

Lagidium viscaccia cuscus. BOLIVIA. Department of Cochabamba, 9.5 km by road SE of Rodeo, then 2.5 km on road to ENTEL antenna, 3875 m (260946 AMNH).

Lagostomus maximus. BOLIVIA. Department of Chuquisaca; 4.5 km by road W of Carandayti, 500 m (262295–262287 AMNH). BOLIVIA. De-

partment of Tarija, 55.2 km by road E of Tiquipa, 528 m (246958 AMNH).

Microcavia niata. BOLIVIA. Department of Oruro; 30 km S and 25 km E of Sajama, 3850 m (263000 AMNH).

Octodon degus. CHILE. Province of Santiago; Fundo Santa Laura, 10 km W of Tiltil, 1000 m (150079 MVZ).

Octodontomys gliroides. BOLIVIA. Department of La Paz; Caracato, 2900 m (249052 AMNH).

Oxymycterus paramensis. BOLIVIA. Department of Cochabamba, 15 mi ESE of Tiraque, 10,500 ft (119947 MVZ).

Proechimys sp. BRASIL. Rio Tapajoz, Igarape Javary (137221 AMNH).

Spalacopus cyanus. CHILE. Province of Cautin; Papudo, 30 m (33277 AMNH).

Thrichomys apereoides. BOLIVIA. Department of Santa Cruz; 7 km N and 38 km W of Robore (AMNH 260860).